

ADAPTIVE SIGNIFICANCE OF ELABORATE PLUMAGE WHEN
EXPRESSED IN BOTH SEXES:
MULTIPLE FUNCTIONS OF THE RACKETED-TAIL OF THE
TURQUOISE-BROWED MOTMOT (*EUMOMOTA SUPERCILIOSA*)

A Dissertation
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by
Troy Ganem Murphy
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Troy Ganem Murphy, Ph.D.

Cornell University 2005

When elaborate plumage is found in sexually dimorphic species, it is thought to be the product of sexual selection. When found in both males and females, this presents a paradox because females generally do not compete for access to mates. Why then are males and females of many species adorned with elaborate plumage? To address this question, I investigated the adaptive function of the male and female racketed-tail of the turquoise-browed motmot (*Eumomota superciliosa*).

I tested the hypotheses that the tail functions as a sexually- or socially-selected character in both sexes, or in only males. I found that motmots do not pair assortatively for tail-plumage, and that males with the most elaborate tails were in better phenotypic condition, had greater pairing success, and had greater fledgling success. There was no relationship between female tail-plumage and these measures. These results support the hypothesis that tail-plumage functions as a sexually- or socially-selected character in males, but not in females.

Why then do female motmots also have a long racketed tails if they do not gain sexually- or socially-selected benefits from maintaining the tail? The answer rests with the naturally selected function of the tail: When motmots detect predators, both sexes of perform a wag-display,

whereby the long racketed-tail is repeatedly rocked side-to-side in a pendulous fashion. I demonstrated that the wag-display is performed in the same manner when motmots were: (i) together or away from conspecifics; (ii) paired or unpaired; (iii) together or away from their mates. These results support the hypothesis that the predator-elicited wag-display is oriented to the predator, and functions as a pursuit-deterrent signal.

I propose that both male and female turquoise-browed motmots have been selected to maintain long tails for pursuit-deterrent signaling, yet males have been subject to the additional force of sexual- or social-selection, and this explains why male tail-plumage is approximately 10% larger than female tail-plumage.

BIOGRAPHICAL SKETCH

Troy Murphy was born in Phoenix, Arizona on October 27, 1973. When he came of age, his family wisely fostered his interest in the natural world by buying him a much-wanted bb-gun. Through the sites, Troy educated himself on the lives of animals as he spent countless hours tracking, watching, and studying (not to mention shooting) the critters that inhabited the mountain-park that he considered his back yard.

During Troy's junior year in high school, he was handed a pair of binoculars and was told to watch (and not to shoot) as a white-breasted nuthatch corkscrewed its way up a tree. Much greater detail was visible through the binoculars than through the small scope on the bb-gun, so the next day Troy bought a bird guide, and retired his bb-gun to the closet.

Troy enrolled at the University of Arizona and instantly fell in love with the biological-sciences. His first research position brought him to Washington to study spotted owls, where, to everyone's amusement, his owl-hoot sounded like a dying chicken. This formative experience strongly influenced Troy's later decision to study the evolution of visual, and not vocal signals. Also during his undergraduate career, Troy and his best friend Ed Scholes studied bowerbirds in Australia. During the evenings they sat around the campfire eating cabbage and peanuts while learning how to wade through the quagmire of S. J. Gould's essays on evolution. It was during these drawn-out readings that Troy discovered that he was an adaptationist at heart.

In 1996 he earned a degree in ecology and evolutionary biology, and the following year he moved to Ithaca, NY and began his Ph.D. in behavioral ecology at Cornell University.

Soon after moving to Ithaca, Troy pair-bonded with his long-time friend, Nicole L. Mack (now Murphy). Nicole traveled with Troy to the motmot field-site in Yucatan, Mexico, where she was an invaluable asset to the project and to Troy's happiness. In 2002, they were wed, and their reproductive success leapt upward on March 5, 2004, when their wonderful daughter, Alissa P. Murphy was born.

To my parents, for their generous support and love

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In Yucatan, Mexico, I could not have been able to start the project without the help of Barbara MacKinnon de Montes from Conservacion de las Aves (CAPY) and Amigos de Sian Ka'an A.C.. I am also indebted to

the staff at the Ria Lagartos Biosphere Reserve for the use of facilities, and information on the turquoise-browed motmot. The staff at Niños y Crías A.C. became a second family, and I would like to especially thank Dr. Rodrigo Migoya von Bertrab, Mauricio Quijano Farjat, and Melgar J. Tabasco Contreras for the technical support they provided, and also for all the fun times we shared together. I am also thankful to Niños y Crías for the inspiration and great ideas during the filming of the documentary on the motmot. I also would like to thank the landowners in northern Yucatan who kindly allowed me work on their property, and who left the motmots and me undisturbed. I also thank the wonderful town-folk of Rio Lagartos, who made my field-house feel like a home.

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CHAPTER 1

LACK OF ASSORTATIVE PAIRING FOR RACKETED-TAIL IN THE
ELABORATELY PLUMED AND SOCIALLY MONOGAMOUS
TURQUOISE-BROWED MOTMOT

ABSTRACT

Elaborate male and female plumage can be maintained by mutual sexual selection and function as a mate-choice or status signal in both sexes. When both sexes maintain sexually selected characters, assortative pairing for those characters is predicted to occur. Both the male and female turquoise-browed motmot have long tails which terminate in widened, blue-and-black rackets that appear to hang, unattached, below the body of the bird. I tested whether mutual sexual selection maintains the turquoise-browed motmot's elaborate tail-plumage by evaluating the prediction that pairs will form in an assortative manner for tail-plumage. I also tested if assortative pairing occurs for body-size, a potential measure of dominance, and for phenotypic condition, a measure of individual quality. Assortative pairing was investigated: (1) among all pairs within the study population, (2) among newly formed pairs, and (3) among experimentally induced pairs that formed after I removed females from stable pairs. Assortative pairing was not found for tail-plumage, body-size, or phenotypic condition in any of these three samples. Thus, the mutual sexual selection hypothesis was not supported. I discuss the possibility that the tail is sexually selected in only males, and I present hypotheses for the evolutionary maintenance of the elaborate female tail.

INTRODUCTION

When males express elaborate plumage characters and females are undecorated or drab, it is likely that sexual selection maintains the elaborate male characters (Darwin, 1871; for review see Andersson, 1994). However, there are many species with elaborate characters in both sexes. Elaborate males and females are found in a diverse array of avian taxonomic groups, including penguins, grebes, swans/ducks, alcids, parrots, jays, flycatchers, waxwings, and swallows, and motmots, and these groups are of great interest because elaborate female plumage is difficult to reconcile within the traditional framework of sexual selection (Amundsen, 2000a).

Sexual selection may favor the expression of elaborate characters in males and females when competition for access to mates occurs in both sexes (i.e., mutual sexual selection -- Jones and Hunter, 1993, Johnstone et al., 1996; Johnstone, 1997). Male and female competition for mates is expected to occur when the potential reproductive rate is similar for both sexes (Clutton-Brock and Vincent, 1991), and when the operational sex ratio is near unity, as neither sex will represent a scarcer resource to be competed over by a limited sex (Emlen and Oring, 1977). Because the potential reproductive rate and the operational sex ratio are highly dependant on the relative degree of male and female parental investment, mutual sexual selection is expected to operate most strongly on socially monogamous species with obligate biparental care (Burley, 1986).

Many investigations into the function of elaborate male and female plumage in socially monogamous species have supported the mutual

sexual selection hypothesis by demonstrating that males and females pair assortatively (Andersson et al., 1998, Daunt et al., 2003, Jawor, 2003; Massaro et al., 2003; Møller, 1993; Potti and Merino, 1996). Assortative pairing for sexually selected characters occurs when individuals prefer to mate with the most ornamented mate available, and high quality mates accept only high quality suitors. This leaves lower-quality individuals to mate amongst themselves, not because they prefer to mate assortatively, but because their own low quality precludes them from mating with high-quality individuals (Burley, 1983). Assortative pairing can also result if elaborate characters function as sexually selected status signals in both sexes, as males and females compete with same-sex rivals to gain access to the same resources (Creighton, 2001).

In this study, I investigate the function of the elaborate male and female tail-plumage of the turquoise-browed motmot. Because the turquoise-browed motmot is a socially monogamous species that exhibits bi-parental care, I hypothesized that the tail-plumage is a mutually sexually selected character. The male and female tail is long --comprising approximately sixty percent of the total body length-- and terminates in widened, blue-and-black rackets, which appear to hang, unattached, below the body of the bird. The apparent detachment occurs because the rachises of the central tail-feathers are devoid of barbs for approximately one-third of the feather above the terminal racket-flags.

I tested the prediction that pairs will form assortatively for tail-components by measuring the similarity of tail-plumage among mated pairs: (1) among all pairs in the study-population, and (2) among newly formed pairs. These two groups were analyzed separately because motmots exhibit

high mate fidelity and survival (unpublished data), which restricts the pool of available mates each season. Thus, to detect assortative pairing among individuals who compete for mates within the restricted pool, it was necessary to study pairing patterns of newly formed pairs. In addition to these correlative studies, I (3)) experimentally removed females from stable pair-associations and monitored whether replacement females paired assortatively for tail-plumage with their new mates. In all the above samples, I also investigated pairing patterns for body size, a potential measure of dominance, and for phenotypic condition, a measure of individual quality.

In addition, I quantified sexual dimorphism and dichromatism (within the avian visual range (300-700 nm)) to evaluate if selection for ornamentation operates similarly on the sexes. I also measured how tail-plumage changed with age.

MATERIALS AND METHODS

Study organism and study site

The turquoise-browed motmot breeds colonially in the Yucatan Peninsula of Mexico in sinkholes, fresh-water wells, limestone quarries, and ancient man-made structures (e.g. Maya ruins; Scott and Martin, 1983). Colony sizes ranged from 2 to 60 pairs, with colonies of 10-20 pairs being most common (Orejuela, 1977). Nest tunnels are dug into vertical earthen banks (0.4 - 2.2 m in depth, mean = 1.3 m).

I studied motmots at seven colonies during the breeding seasons (March-August) of 1999-2002; four in abandoned limestone quarries (range = 7 - 39 pairs), and three in fresh-water wells (approximate range 20-30 pairs). All colonies were located within a 10 sq km area near the

Ria Lagartos Biosphere Reserve, in Northern Yucatan, Mexico (21° 33' N, 88° 05' W). The area is characterized by thorn-scrub forest and grazing pastureland, and experiences a long dry season (Dec-May).

The species is migratory, and individuals spend six months on wintering grounds, presumably in moist forests in the center of the Yucatan Peninsula, and then arrive at the breeding areas three months before the commencement of clutch-initiation (late May or early June). Upon arrival, many pairs form immediately. Some pairs are already formed on arrival. Otherwise, pair-formation occurs over approximately a one-month period, during which time it is common for pair associations to shuffle as new individuals arrive and compete for nesting territories and partners. Each year, an equal ratio of males and females fail to pair and remain as “floaters” at the nesting colonies throughout the breeding season (Chapter 2).

Motmots were captured in mist nets prior to the start of clutch-initiation (April-May). Sex was determined by laparotomy. There were no noticeable negative affects from the procedure: laparotomized individuals were observed at the breeding colonies the following day behaving normally. To facilitate individual identification, most breeders (98%) and approximately 85% of non-breeding floaters were color-banded at the four colonies located in limestone quarries.

Morphological measurements

Morphological measures were taken from all birds in 1999-2002. Linear measures were taken to the nearest 0.1 mm with calipers or with a ruler. Mass was measured with a Pesola scale to the nearest 0.5 g. Tarsus

length, bill length, and flattened wing chord length were measured, and values were combined using principal component analysis to compute a single body-size index (PC1). The first principal component (PC1) explained 53% of the variation in body size. I measured six linear components of the tail (Figure 1.1): 1) Total Tail (central-follicle to the distal tip of the longest central rectrix), 2) Racket (the sum of the Wire (the feather-stem devoid of barbs) and the Flag (the oval shaped tip); 3) Base (central-follicle to the distal tip of the longest second feather -- the tail is graduated, so second feathers are the next longest feathers after the racketed central tail feathers), 4) Wire (the length of rachis devoid of barbs between the distal tip of the Base and the proximal tip of the Flag on the longest central rectrix), 5) Blue of Flag (blue portion of the dorsal surface of the Flag on the longest central rectrix), and 6) Black of Flag (the distal black portion of the dorsal surface of the Flag on the longest central rectrix).

I also measured the surface area of the oval-shaped tip of the largest Flag, herein referred to as 7) Area Flag. In 2002, I photographed feathers using standardized digital photography, and included a size reference. Surface area was later calculated with the ImageJ Software Package (U. S. National Institutes of Health, 1997-2005). I calculated Area Flag for other years by multiplying the length of Flag by its linear width (measured by flattening the Flag with a ruler). The calculated measures were significantly and highly correlated with the measures taken from photographs ($F = 1578.74$, $p < 0.0001$, $r^2 = 83.0$, $n = 324$). Thus, the two types of measures were considered equivalent, and calculated measures were used when photographic measures were unavailable.

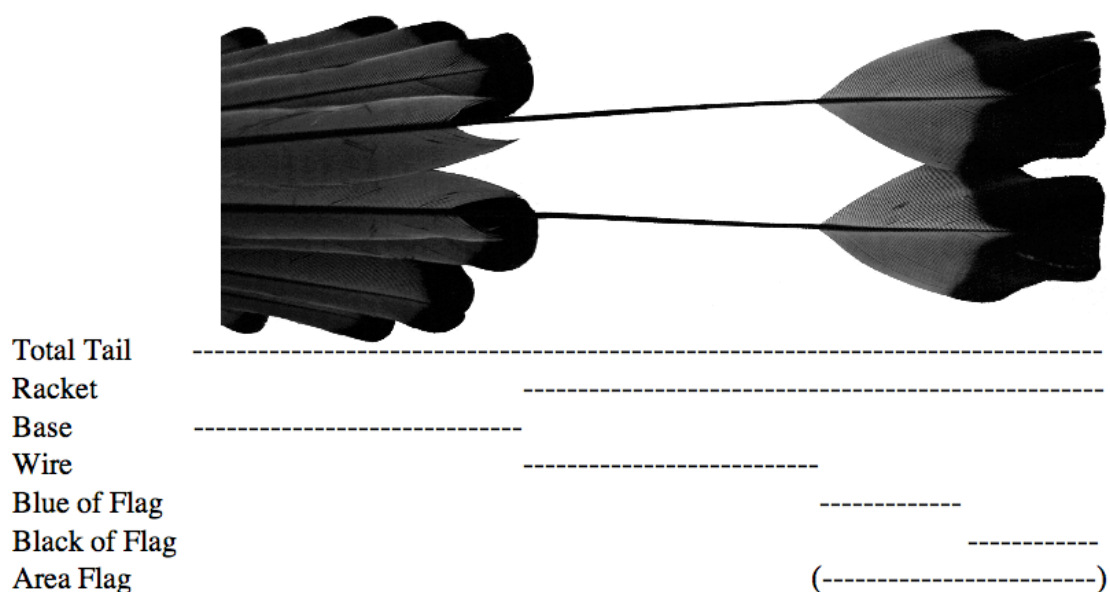


Figure 1.1. Tail-components of the turquoise-browed motmot. The horizontal lines define the linear distance measured for each tail-component. Area Flag was measured as surface-area using standardized digital photography, or by multiplying the Flag's width by its length.

Only I collected morphological measurements, and repeatability (the intraclass correlation coefficient) was calculated on a subset of birds in 2002 by measuring the same individual on different days (after Lessells and Boag, 1987). Repeatability was high for all linear measures of tail-components ($R \geq 0.94$, $n = 15$), and also for surface-area ($R = 0.89$, $n = 15$).

Phenotypic condition measurements

I collected five measures of phenotypic condition from each bird: (i) Size-specific mass. I calculated residuals from the regression of mass on body size to evaluate mass while controlling for skeletal size (Jakob et al., 1996); (ii) Hematocrit. I measured percent erythrocytes in blood samples (year 2002 only; following methods of chapter 2); Hematocrit is a widely used serological test to assess a bird's health status (Bush, 1975; Amand, 1986), and can also reflect recent metabolic activity (Palomeque and Planas, 1978; Saino et al., 1997); (iii) Ectoparasite load. Motmots were parasitized by *Philopterus* sp. feather lice (identified with Price et al., 2003). I quantified the degree of *Philopterus* louse infestation by counting eggs, which are laid almost exclusively in the black feathers of the chest-badge (following methods of chapter 2). *Philopterus* lice have been shown to have a negative effect on their host by reducing feather mass and survival in rock doves (Clayton et al., 1999) and by reducing nutritional condition in magpies (Blanco et al., 2001); (iv) Growth bars. I calculated average growth-bar distance by measuring the distance between 5-7 bars on the blue region of the Flag (following methods of chapter 2). Growth-bar distance represents the amount of feather growth

over a twenty-four hour period, and indicates the amount of energy reserves that were available during molt (Grubb, 1989; 1991); (v) Fluctuating asymmetry. I quantified fluctuating asymmetry as the absolute value of the difference in length of the two central rectrices. Body-size was not correlated with asymmetry, so did not bias measures (asymmetry was not correlated with body-size (PC1): male: $F = 0.43$, $p = 0.51$, $n = 48$; female: $F = 0.05$, $p = 0.82$, $n = 52$). Symmetrical growth indicates developmental homeostasis, and individuals with lower phenotypic condition are generally less symmetric (Møller, 1990; Van Valen, 1962).

Differentiation of age-classes

Adults and yearlings were differentiated based upon tail feather wear. Tail feathers of known age-yearlings were extremely worn and abraded (Figure 1.2). Apparently yearlings do not molt their tail feathers before their first breeding season, so when they return to the breeding grounds, they still have their initial set of tail-feathers (feathers from when they were in the abrasive, earthen nest). Two lines of evidence supported this hypothesis: 1) 100% ($n = 75$) of individuals who had worn feathers when originally captured, had non-worn tails in all subsequent years, 2) 82% (14/17) of birds banded as nestlings returning the following year had worn tail feathers. Because some yearlings molted their tail feathers (probably due to accidental tail loss), I may have incorrectly aged some molted yearlings as adults; for example, one nestling lost two tail feathers upon capture from the nest, and the following year these feathers had

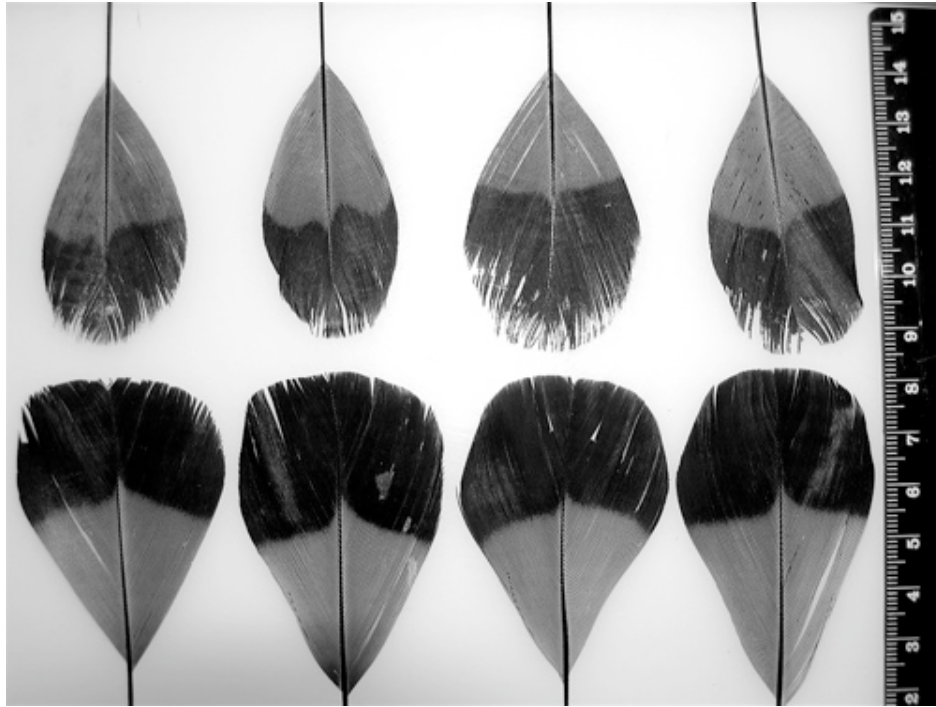


Figure 1.2. The Flag of four adult males (bottom row), and four yearling males (top row). Female adults and yearlings show the same pattern. Yearling feathers are worn, which is caused by abrasion of the feather upon the earthen nest during the nestling period the previous breeding season.

regrown and were not worn, while all other tail feathers were worn. However, birds with worn tail feathers were unambiguously yearlings.

Assortative pairing: General methods

Pairs were identified by behavioral observations at four colonies located within limestone quarries. Observations were conducted with spotting scopes from within a permanent blind located 45-55m from each colony. Because some male-female associations were unstable during the long three-month pre-breeding season, I only analyzed assortative pairing among birds that initiated a breeding attempt together, as these pairs represent the ultimate outcome from competition for mates.

I compared the similarity of three variables within each pair: (1) tail-component size, (2) body size-index (PC1), and (3) the five measures phenotypic condition. To control for potential effects of tail-feather loss on pairing patterns and phenotypic condition, I excluded pairs where one or both members of a pair lost both central tail-feathers before the pair formation (2001: 4 pairs, 2002: 1 pair).

Assortative pairing: (1) among all pairs within study population

In 2002, I compared the similarity among all paired birds comprised of (1) two adults, two yearlings, and mix-aged pairs ($n = 60$ pairs), and (2) only adult pairs ($n = 53$ pairs). The later analysis was conducted to separate assortative pairing for age from assortative pairing for tail-components (i.e., because yearlings have smaller tail-components (see results), assortative pairing for age could be mistaken for assortative pairing for tail-components.).

Assortative pairing: (2) among newly formed pairs

Using a combined data set from 2001 and 2002, I compared the similarity among paired birds from newly formed pairs: (1) comprised of two adults, two yearlings, and mix-aged pairs ($n = 53$ pairs), and (2) only adult pairs ($n = 45$ pairs).

Assortative pairing: (3) after experimental removal of females

I permanently removed 12 females from one colony by capturing them and transporting them ~100 km away. Females were removed from pairs that were stable for at least 30 days, and females were removed over a four-day period immediately before clutches were initiated. After removal, all of the males who lost mates successfully re-paired with females from the “floater” population. I compared tail-components, body-size, and phenotypic condition of males and females within the newly formed pairs.

Sexual dimorphism

The analyses of sexual dimorphism were based on measurements taken in 2002. Linear morphological measurements were made on 147 adult males, 122 adult females. Surface area measurements were calculated for 135 adult males, 112 adult females, 32 yearling females, and 41 yearling males. In addition, I computed correlations among the seven measures of tail-components to understand how each individual's tail-components were intercorrelated.

Sexual dichromatism

The analyses of sexual dichromatism were based on measurements taken in 2000 and 2002 from tail-feathers collected from 75 adult males and 58 adult females. Reflectance measures were taken from the Blue of Flag. I measured reflectance with an Ocean Optics USB2000 spectrometer and PX-2 pulsed xenon lamp (Ocean Optics Inc., Dunedin, USA) by placing the sensor and light source perpendicular to the feather. Reflectance data represent proportion of reflectance compared to a Spectralon white standard (Labsphere Inc., New Hampshire, USA). Reflectance was calculated at 3.7 nm intervals across the avian visual range (300-700 nm).

Reflectance was measured from both the left and right side of the rachis, and I calculated the mean of five measures for each feather, and when both feathers were available, I calculated the mean reflectance from both central tail-feathers. Hue, brightness, and UV chroma were computed for each individual. Because the reflectance spectrum of the tail is bimodal (see results, Figure 1.3), with one peak in the UV and another peak in the blue-green, hue (spectral location) was measured separately for UV and for blue-green. Hue was calculated as the wavelength corresponding with the maximum reflectance within each spectral region (UV: 300-400 nm; blue-to-red: 400-700nm). Brightness (spectral intensity) was calculated as the total reflectance between 300-700 nm. UV Chroma (spectral purity or saturation) was calculated as the proportion of total reflectance occurring between 300-400 nm.

Only I collected reflectance measurements, and repeatability was calculated on a subset of 15 birds by measuring the same feather on

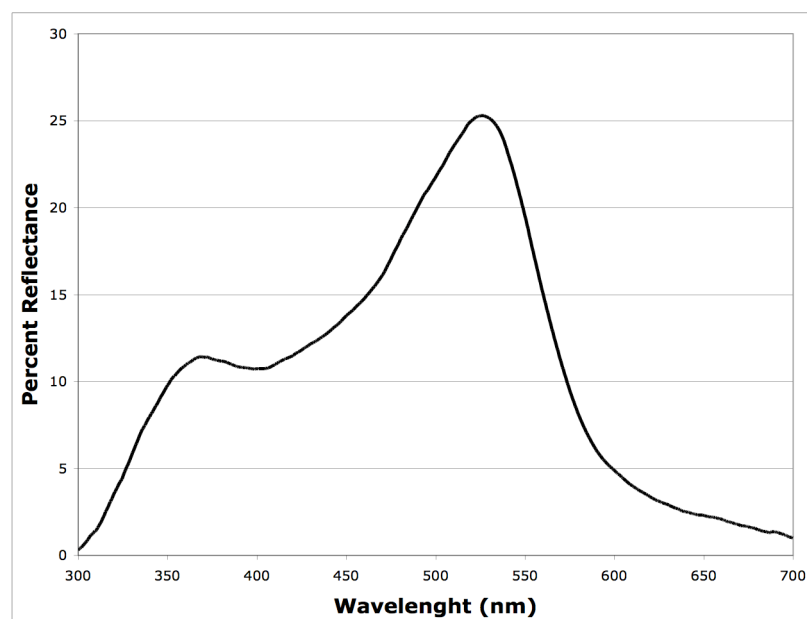


Figure 1.3. Reflectance spectrum from the Blue of Flag of a typical male or female turquoise-browed motmot. The spectrum of the tail plumage is bimodal, with one peak in the UV and another larger peak in the blue-green.

different days (after Lessells and Boag, 1987). Repeatability was high for all reflectance measures ($R \geq 0.81$, $n = 15$).

Change in morphology with age

To investigate if tail-component size, or body-size increased with age, I measured the between-year change in: (1) yearlings, and (2) in adults. Among yearlings, I compared measures taken when they were originally captured to when they were recaptured the following year. Between-year data were pooled from 1999-2000, 2000-2001, and 2001-2002 ($n =$ males: 24; females: 35). Among adults, I compared measures taken when they were captured for the first time, and when the same birds were recaptured the following year. Between-year data were pooled from 1999-2000, 2000-2001, and 2001-2002 ($n =$ males: 47, females: 44).

Statistics

Assortative pairing among 1) all pairs within the study population, and 2) among newly formed pairs, were analyzed by correlating measures (tail-components, body-size, and phenotypic condition) among pairs with pairwise correlation analysis. For the female-removal experiment, assortative pairing was analyzed by ranking measures (tail-components, body-size, and phenotypic condition) within a sex, and then by comparing the ranks of pairs with spearman rank correlations. Measures of fluctuating asymmetry were log transformed to fulfill assumptions of normality.

Sexual dimorphism was analyzed with ANCOVA, with body-size (PC1) as a covariate to control for sexual differences in body-size.

Correlations among tail-components, and between body-size and tail-components were investigated with pairwise correlation analysis.

ANOVA was used to investigate sexual differences in body-size, and dichromatism.

Repeat-measure ANOVA was used to analyze change in body-size and tail-components between years, and year was placed in the model to control for potential non-age related differences in tail-expression between multiple years. Adjusted r^2 are reported.

Sequential Bonferroni corrections (Holm, 1979) were applied to all analysis where multiple tests applied to the same data set, and corrections were applied separately for the sexes. Sample sizes for analyses are limited to pairs for which I have morphological or phenotypic condition measures for both members of the pair. All statistical analyses were two tailed, and rejection level was set at $p > 0.05$. Descriptive statistics are listed as mean \pm standard error.

RESULTS

Assortative pairing: (1) among all pairs within study population

Yearlings included

There was no significant relationship between tail-components of all pairs in the population. However, there was a non-significant trend for pairs to have a similarly sized Area Flag ($F = 6.64$, $p = 0.0127$, $r^2 = 0.11$, $n = 56$, which was non-significant after sequential Bonferroni correction on seven tests of tail-components (Holm, 1979; Table 1.1a). There also was a non-significant trend for pairs to have similar body-size (PC1); however, body-size explained only a small amount of variation in pairing

Table 1.1. Correlation coefficients of tail-components, body-size, and phenotypic condition among all pairs in 2002 {(a) pairs with yearling(s) included, (b) pairs with yearling(s) excluded}. No assortative pairing was found: correlation coefficients are low for the comparison between identical measures (along grey diagonal), and p-values along diagonal were non-significant after sequential Bonferroni correction, which was applied separately to analysis on males and females. Sample sizes for analyses ranged between 52 - 63 pairs.

MALE**FEMALE**

	Total Tail	Racket	Base	Wire	Blue of Flag	Black of Flag	Area Flag	Body-size (PC1)	Size-specific mass	Hematocrit	Ectoparasite load	Growth-bar	Asymmetry
Total Tail	0.00	-0.03	0.04	-0.19	0.18	0.15	0.29						
Racket	-0.08	-0.07	-0.04	-0.22	0.12	0.18	0.20						
Base	0.12	0.06	0.14	-0.03	0.13	0.04	0.26						
Wire	-0.06	-0.03	-0.06	-0.19	0.17	0.14	0.15						
Blue of Flag	-0.09	-0.12	0.01	-0.05	-0.07	-0.08	0.07						
Black of Flag	0.07	0.07	0.02	0.04	-0.11	0.20	0.03						
Area Flag	0.09	-0.06	0.22	-0.13	0.07	0.09	0.33						
Body-size (PC1)								0.25					
Size-specific mass									0.02	0.02	-0.03	0.13	0.08
Hematocrit									0.01	0.15	0.08	-0.06	0.03
Ectoparasite load									0.02	-0.15	0.31	-0.15	-0.06
Growth-bar									-0.14	0.02	0.02	0.01	0.11
Asymmetry									0.16	-0.23	0.04	0.03	-0.19

1.1a

MALE**FEMALE**

	Total Tail	Racket	Base	Wire	Blue of Flag	Black of Flag	Area Flag	Body-size (PC1)	Size-specific mass	Hematocrit	Ectoparasite load	Growth-bar	Asymmetry
Total Tail	0.02	-0.01	0.05	-0.17	0.14	0.17	0.29						
Racket	-0.08	-0.10	-0.01	-0.26	0.10	0.24	0.28						
Base	0.17	0.14	0.12	0.11	0.08	-0.02	0.10						
Wire	-0.06	-0.04	-0.05	-0.22	0.15	0.22	0.25						
Blue of Flag	-0.11	-0.16	0.02	-0.04	-0.11	-0.14	-0.02						
Black of Flag	0.09	0.07	0.07	0.04	-0.08	0.16	0.02						
Area Flag	0.09	-0.01	0.15	0.02	0.00	-0.05	0.09						
Body-size (PC1)								0.20					
Size-specific mass									-0.18	0.02	-0.12	0.00	0.12
Hematocrit									-0.10	0.21	-0.02	-0.23	0.01
Ectoparasite load									-0.06	-0.26	0.25	-0.19	-0.02
Growth-bar									-0.10	0.00	-0.05	0.11	0.12
Asymmetry									0.20	-0.18	-0.07	-0.14	-0.23

1.1b

patterns ($F = 3.50$, $p = 0.0664$, $r^2 = 0.06$, $n = 59$; Table 1.1a). There was no significant relationship between phenotypic condition of pairs. But, there was a non-significant trend for pairs to have similar ectoparasite loads ($F = 5.97$, $p = 0.0176$, $r^2 = 0.09$, $n = 59$, which was non-significant after sequential Bonferroni correction on five tests of phenotypic condition (Holm, 1979; Table 1.1a).

Adults only

There were no significant relationships between tail-components, body-size (PC1), or phenotypic condition of adult pairs (Table 1.1b).

Assortative pairing: (2) among newly formed pairs

Yearlings included

There was no a significant relationship between tail-components of newly formed pairs. There was a non-significant trend for these pairs to have a similarly sized Area Flag ($F = 4.01$, $p = 0.0551$, $r^2 = 0.13$, $n = 30$), and a dissimilarly sized Racket ($F = 5.17$, $p = 0.0272$, $r^2 = 0.09$, $n = 53$), both of which were non-significant after sequential Bonferroni correction on seven tests of tail-components (Holm, 1979; Table 1.2a). There were no significant relationships between body-size (PC1) or phenotypic condition of these pairs (Table 1.2a).

Adults only

There was no significant relationship between tail-components of adult pairs, although there was a non-significant trend for these pairs to have a dissimilarly sized Racket ($F = 6.18$, $p = 0.0168$, $r^2 = 0.13$, $n = 45$, which was non-significant after sequential Bonferroni correction on seven tests of tail-components (Holm, 1979; Table 1.2b). There were no

Table 1.2. Correlation coefficients of tail-components, body-size, and phenotypic condition among newly formed pairs in 2000 and 2001 {(a) pairs with yearling(s) included, (b) pairs with yearling(s) excluded}. No assortative pairing was found: correlation coefficients are low for the comparison between identical measures (along grey diagonal), and p-values along diagonal were non-significant after sequential Bonferroni correction, which was applied separately to analysis on males and females. Sample sizes for analysis on hematocrit (measured only in 2002) ranged between 27 - 30 pairs, and sample sizes for all other analyses ranged between 44 - 53 pairs.

MALE**FEMALE**

	Total Tail	Racket	Base	Wire	Blue of Flag	Black of Flag	Area Flag	Body-size (PC1)	Size-specific mass	Hematocrit	Ectoparasite load	Growth-bar	Asymmetry
Total Tail	-0.14	-0.23	0.06	-0.33	0.04	0.24	0.26						
Racket	-0.25	-0.30	-0.04	-0.36	0.05	0.13	0.17						
Base	0.10	-0.01	0.20	-0.11	-0.05	0.31	0.28						
Wire	-0.13	-0.14	-0.02	-0.20	0.11	0.05	0.13						
Blue of Flag	-0.02	-0.15	0.12	-0.22	0.08	0.12	0.18						
Black of Flag	-0.30	-0.26	-0.20	-0.16	-0.25	0.07	-0.09						
Area Flag	-0.03	-0.19	0.16	-0.27	-0.03	0.30	0.35						
Body-size (PC1)								0.01					
Size-specific mass									0.19	0.06	0.21	-0.15	-0.15
Hematocrit									0.27	-0.21	0.00	0.12	-0.28
Ectoparasite load									0.12	-0.07	0.08	-0.01	0.08
Growth-bar									-0.29	0.04	0.12	-0.08	0.30
Asymmetry									-0.04	-0.33	-0.08	0.19	-0.22

1.2a

MALE**FEMALE**

	Total Tail	Racket	Base	Wire	Blue of Flag	Black of Flag	Area Flag	Body-size (PC1)	Size-specific mass	Hematocrit	Ectoparasite load	Growth-bar	Asymmetry
Total Tail	-0.14	-0.25	0.09	-0.32	-0.05	0.25	0.19						
Racket	-0.26	-0.35	0.01	-0.42	0.01	0.17	0.30						
Base	0.16	0.09	0.20	0.08	-0.19	0.27	-0.18						
Wire	-0.13	-0.16	0.01	-0.26	0.08	0.16	0.45						
Blue of Flag	-0.02	-0.16	0.15	-0.19	0.04	0.02	-0.12						
Black of Flag	-0.30	-0.28	-0.18	-0.15	-0.23	-0.03	-0.31						
Area Flag	-0.15	-0.19	-0.04	-0.05	-0.30	0.05	-0.22						
Body-size (PC1)								-0.07					
Size-specific mass									0.08	0.07	0.20	-0.31	-0.14
Hematocrit									0.12	-0.19	-0.30	-0.27	-0.39
Ectoparasite load									0.16	-0.24	-0.01	0.05	0.12
Growth-bar									-0.28	-0.02	0.03	0.01	0.32
Asymmetry									-0.07	-0.23	-0.21	0.02	-0.25

1.2b

significant relationships between body-size (PC1), or phenotypic condition of these pairs (Table 1.2b).

Assortative pairing: (3) after experimental removal of females

All (12/12) of the males whose partners were removed in the female-removal experiment re-paired and initiated a clutch. Replacement females came from the floater population.

There was no significant relationship between tail-components of the replacement females and the original males (Tail: $r = 0.08$, $p = 0.83$; Racket: $r = 0.34$, $p = 0.34$; Base: $r = 0.03$, $p = 0.93$; Wire: $r = 0.28$, $p = 0.43$; Blue of Flag: $r = -0.02$, $p = 0.95$; Black of Flag: $r = -0.47$, $p = 0.17$; Area Flag: $r = -0.26$, $p = 0.47$; $n = 10$ for all comparisons). There were no significant relationships between body-size of the replacement females and the original males ($r = 0.18$, $p = 0.63$, $n = 10$), nor between phenotypic condition of the replacement females and the original males (size-specific mass: $r = 0.52$, $p = 0.18$; Hematocrit: $r = -0.43$, $p = 0.34$; Ectoparasite load: $r = -0.02$, $p = 0.95$; Growth-bar distance: $r = 0.54$, $p = 0.21$; Fluctuating asymmetry: $r = 0.33$, $p = 0.36$; $n = 10$ for all comparisons).

Sexual dimorphism

Males were significantly heavier, and larger (PC1) than females (Table 1.3). Most tail-components were also significantly larger in males after controlling for the sexual difference in body size (Table 1.3). The sexual dimorphism index (SDI) (computed as mean male / mean female) for tail-components covered a large range (SDI = 1.0 - 1.10), with a low degree of dimorphism for Total Tail (SDI = 1.03) and a larger amount of

Table 1.3. Adult sexual dimorphism in mass, body-size, and tail-components. The sexual dimorphism index was computed as (SDI = mean male / mean female). Males are larger, and have larger tail-components (body-size index (PC1) was included as a covariate in analysis of sexual dimorphism of tail-components). Significance indicated (* or ns) after sequential Bonferroni correction. Coefficient of variation (CV) is listed for each measure. Wire and Area Flag are expressed with the largest amount of variation. Sample sizes are listed in parenthesis.

Morphology	Male		Female		Sexual difference			
	Mean	CV	Mean	CV	SDI (m/f)	F	p	sig
Mass (g)	67.6 (147)	5.2	66.0 (104)	3.2	1.02	14.35	0.0002	*
Tarsus (mm)	23.3 (146)	2.8	23.2 (122)	2.6	1.00	2.99	0.08	ns
Bill (mm)	33.5 (146)	3.6	32.8 (122)	3.6	1.02	23.92	<.0001	*
Wing (mm)	122.6 (147)	2.1	121.7 (122)	1.8	1.01	8.20	0.0045	*
Body-size (PC1)	(144)		(118)			19.42	<.0001	*
Total Tail (mm)	213.9 (146)	3.4	207.8 (117)	3.2	1.03	32.13	<.0001	*
Racket (mm)	109.1 (140)	5.2	103.6 (115)	4.7	1.05	74.12	<.0001	*
Base (mm)	105.4 (142)	3.6	105.8 (117)	3.1	1.00	3.93	0.05	ns
Wire (mm)	52.1 (140)	10.1	47.4 (116)	9.6	1.10	39.94	<.0001	*
Blue of Flag (mm)	30.5 (140)	7.7	28.9 (112)	8.8	1.06	21.00	<.0001	*
Black of Flag (mm)	26.5 (140)	7.2	26.3 (112)	7.4	1.01	0.07	0.80	ns
Area Flag (cm ²)	14.7 (135)	9.9	13.8 (112)	9.2	1.07	18.74	<.0001	*

dimorphism for Wire (SDI = 1.10) and Area Flag (SDI = 1.07). Two tail-components that were not significantly sexually dimorphic were Base and Black.

Body size characters were expressed with little variation (CV = 1.8 - 3.6), whereas variation in tail-components covered a broad range (CV = 3.1 - 10.2). Wire and Area Flag represented the most variable tail-components in both sexes, and were significantly more variable than body size measures ($p \leq 0.001$ in all comparisons). Variation in body-size characters and tail-components was significantly similar in the sexes (test for coefficients of variation: Sokal and Braumann (1980); $p > 0.05$ in all comparisons; Table 1.3).

Many of the tail-components were highly and significantly inter-correlated in both sexes (Table 1.4). Male body-size was significantly correlated with all male tail-components except Blue of Flag; whereas female body-size was only significantly correlated with female Total Tail (Table 1.5).

Sexual dichromatism

The reflectance spectrum of the tail was bimodal (Figure 1.3), with one peak in the UV, and another larger peak in the blue-green. Male and female tail feathers had significantly similar hue in the UV, and in the blue-green, and there were no significant sexual differences in brightness and UV chroma (Table 1.6).

Variation in coloration, as indicated by coefficient of variation was significantly similar in the sexes ($p > 0.05$ in all comparisons) (Table 4). Variation in color covered a wide range (CV = 1.6 - 16.0). Hue was

Table 1.4. Product moment correlations between adult male tail-components (above), and between adult female tail-components (below). Many tail-components are significantly intercorrelated within each sex. (*) indicates significant correlation after sequential Bonferroni correction, which was applied separately to analysis on males and females. See Table 1.1 for sample sizes.

		Total Tail	Racket	Base	Wire	Blue of Flag	Black of Flag	Area Flag
MALE	Total Tail	1						
	Racket	0.87 *	1					
	Base	0.68 *	0.24 *	1				
	Wire	0.70 *	0.87 *	0.09	1			
	Blue of Flag	0.17	0.16	0.15	-0.21	1		
	Black of Flag	0.25 *	0.17	0.23	-0.11	-0.15	1	
	Area Flag	0.26 *	0.19	0.22	-0.22	0.53 *	0.58 *	1
FEMALE	Total Tail	1						
	Racket	0.87 *	1					
	Base	0.71 *	0.28 *	1				
	Wire	0.66 *	0.85 *	0.08	1			
	Blue of Flag	0.27 *	0.25	0.20	-0.16	1		
	Black of Flag	0.24	0.17	0.23	-0.06	-0.34 *	1	
	Area Flag	0.42 *	0.29 *	0.39 *	-0.12	0.46 *	0.40 *	1

Table 1.5. Product moment correlations between body-size (PC1) and adult tail-components (male above, female below). Body-size is intercorrelated with many male tail-components, and is only intercorrelated with female Total Tail. (*) indicates significant correlation after sequential Bonferroni correction, which was applied separately to analysis on males and females. See Table 1.1 for sample sizes.

	Total Tail	Racket	Base	Wire	Blue of Flag	Black of Flag	Area Flag
Male Body-size	0.47 *	0.38 *	0.33 *	0.30 *	0.02	0.22 *	0.19 *
Female Body-size	0.27 *	0.20	0.23	0.10	0.09	0.14	0.16

Table 1.6. Sexual dichromatism of adult tail-feathers. The sexual dimorphism index was computed as (SDI = mean male / mean female). There were no significant differences in measures of dichromatism after sequential Bonferroni correction, which was applied separately to analysis on males and females. Coefficient of variation (CV) is listed for each measure. Sample sizes are listed in parentheses.

Reflectance	Male		Female		Sexual difference			
	Mean	CV	Mean	CV	SDI (m/f)	F	p	sig
Hue: UV	372 (75)	3.2	370 (58)	3.1	1.01	1.23	0.27	ns
Hue: Blue-Green	527 (75)	1.8	526 (58)	1.6	1.00	0.21	0.65	ns
Brightness	12635 (75)	11.3	12050 (58)	12.3	1.04	5.33	0.02	ns
UV Chroma	0.18 (75)	12.5	0.17 (58)	16.0	1.02	0.69	0.41	ns

expressed with little variation in both the UV and blue-green ($CV = 1.6 - 3.2$), whereas brightness and UV chroma were highly variable (Brightness: $CV = 11.3 - 12.3$; UV Chroma: $CV = 12.5 - 16.0$).

Change in morphology with age

Between the first and second year of life, there was a significant increase in male bill and wing length; however there was no significant change in male tarsus. In females, there was a non-significant trend for bill length to increase between years, and a significant increase in wing length; however there was no significant change in female tarsus (Table 1.7). There was a significant change between the first and second year in most tail-components in males and females (Total Tail, Racket, Base, Black of Flag, Area Flag); however, Blue of Flag increased significantly in males, but not in females. There was no significant change in Wire in either sex (Table 1.7).

Among adults, there was a significant increase between years in bill length in males, and a similar, but non-significant pattern in females. There was a significant increase in wing length between years in females, and a similar, but non-significant pattern in males. There was no significant between-year difference in tarsus length in either sex (Table 1.8). Although body-size increased between adult years, there was no significant change between adult years in adult male or adult female tail-components (Table 1.8).

Table 1.7. Change in body-size and tail-components between yearling and second year of life (male on left, female on right). Most tail-components significantly changed between years in males and females. F statistic is from a repeat measure ANOVA. Significance indicated (* or ns) after sequential Bonferroni correction. Sample sizes listed in parentheses.

Morphology	Male				Female			
	yearling to second year				yearling to second year			
	Mean change	F	p	sig	Mean change	F	p	sig
Tarsus (mm)	-0.1	0.72 (22)	0.41	ns	0.0	0.16 (27)	0.70	ns
Bill (mm)	0.7	19.23 (23)	0.0003	*	0.3	4.60 (23)	0.04	ns
Wing (mm)	2.7	103.28 (23)	<.0001	*	2.3	53.10 (23)	<.0001	*
Total Tail (mm)	4.4	33.92 (22)	<.0001	*	5.3	45.99 (29)	<.0001	*
Racket (mm)	2.6	22.75 (22)	<.0001	*	2.7	13.52 (24)	0.0014	*
Base (mm)	2.2	10.59 (22)	0.0042	*	2.9	30.80 (25)	<.0001	*
Wire (mm)	0.3	0.19 (22)	0.67	ns	1.3	1.73 (24)	0.20	ns
Blue of Flag (mm)	1.0	6.80 (19)	0.0190	*	0.1	0.05 (22)	0.83	ns
Black of Flag (mm)	1.2	7.51 (19)	0.0145	*	1.4	9.17 (22)	0.0069	*
Area Flag (cm ²)	2.7	37.64 (13)	<.0001	*	2.3	100.39 (18)	<.0001	*

Table 1.8. Change in body-size and tail-components between adult years of life (male on left, female on right). Tail-components did not significantly change between years in adult males and adult females. F statistic is from repeat measure ANOVA. Significance indicated (* or ns) after sequential Bonferroni correction. Sample sizes listed in parentheses.

Morphology	Male adult to adult year				Female adult to adult year			
	Mean change	F	p	sig	Mean change	F	p	sig
Tarsus (mm)	0.0	0.03 (47)	0.87	ns	0.0	1.53 (43)	0.22	ns
Bill (mm)	0.2	12.32 (40)	0.0008	*	0.1	4.82 (42)	0.03	ns
Wing (mm)	0.6	4.23 (40)	0.05	ns	0.5	10.77 (42)	0.0022	*
Total Tail (mm)	0.7	0.03 (47)	0.86	ns	1.2	2.05 (44)	0.16	ns
Racket (mm)	0.3	0.41 (47)	0.52	ns	0.0	0.03 (44)	0.87	ns
Base (mm)	0.6	3.49 (47)	0.07	ns	1.3	1.58 (44)	0.22	ns
Wire (mm)	-0.3	2.50 (47)	0.12	ns	0.3	0.03 (44)	0.86	ns
Blue of Flag (mm)	0.2	0.40 (39)	0.53	ns	-0.6	0.42 (37)	0.52	ns
Black of Flag (mm)	0.3	0.46 (39)	0.50	ns	0.3	1.60 (37)	0.21	ns
Area Flag (cm ²)	0.1	3.00 (21)	0.11	ns	0.1	1.86 (32)	0.18	ns

DISCUSSION

The adaptive benefits associated with elaborate male and female plumage is of great interest. In some species, elaborate male and female plumage confers sexually selected benefits to both sexes, and the most ornamented males gain access to higher quality females, and the most ornamented females likewise gain access to higher quality males. As a result, pairs form assortatively when both sexes compete for access to mates. Contrary to the prediction of the mutual sexual selection hypothesis, I found no evidence that the elaborately plumed male and female turquoise-browed motmot use their tail-plumage to compete for access to mates: pairs did not form assortatively for tail-components, body-size, or for any of the five measures of phenotypic condition.

The research presented here represents a rather comprehensive test of the assortative pairing prediction. First, I analyzed all pairs in the population, which is the standard method used to detect assortative pairing (Boland et al., 2004; Kraaijeveld et al., 2004; MacDougall et al., 2003; Safran and McGraw, 2004). Second, I looked for assortative pairing among newly formed pairs. The second analysis was well suited to the turquoise-browed motmot because the species is long-lived and has high mate-fidelity. Consequently most motmots re-paired each year, and the pool of available mates was restricted to individuals whose mates had died, individuals who had divorced, and to individuals who were previously unpaired. Thus, variation in quality or tail-plumage was likely limited within this restricted pool. By focusing on the motmots who paired from within the available pool, I should have been able to detect assortative pairing had it occurred. As a third approach, I measured the

similarity of ten pairs that formed after females were removed from stable pair bonds. In this analysis, I compared the rank of tail-component size of the experimental males and replacement females. Again, I should have been able to detect assortative pairing had it occurred.

Although I found no support for the mutual sexual selection hypothesis, there are two line of evidence that suggest that the tail-plumage may function as a sexually selected character in males, but not in females.

First, many of the motmot's tail-components are larger in males than in females. After correcting for larger male body size, the most dimorphic tail-components are Wire, which averages 10% longer in males, and Area Flag, which averages 7% larger in males. The degree to which the sexes differ in expression of elaborate plumage can indicate differences in sexual selection (Darwin, 1871; Höglund, 1989; Dunn et al., 2001), and, the moderate sexual dimorphism in the motmot's Wire and Area Flag may indicate stronger sexual selection on males than on females.

Second, there is considerable variation in the tail-components. The Wire and Area Flag are the most variable, and they are expressed with two to three times greater variation than skeletal features. Variation is expected to be much greater in sexually selected ornaments than in non-ornaments for two reasons: first, because ornament expression is generally condition dependent, and condition itself is widely variable, and second, because ornaments are generally under directional selection (Alatalo et al., 1988; Fitzpatrick, 1997). Skeletal features, in contrast, are generally under stabilizing selection. In fact, the CV of the motmot's Wire (10.1)

and Area Flag (9.9) are high, and are comparable to the mean CV of sexually tail-ornaments reported in long-tailed dimorphic species where males are subject to strong sexual selection (mean CV = 11.6; see Alatalo et al. (1988) for interspecific comparison; see Fitzpatrick (1997) for comparison among Palaearctic birds). The similarity in variation of tail-components in the sexes is difficult to reconcile; however my results agree with some of Fitzpatrick's (1997) findings that males and females with long tails have similar CVs. The mechanisms underlying sexual similarity in character variation requires further study.

The male biased sexual dimorphism in Wire and Area Head, and large amount of variation in Wire and Area Head agree with other research on the turquoise-browed motmot (chapter 2), which supported the hypothesis that sexual selection is operating more strongly upon males. I found that males with the longest Wires were more likely to pair, that they paired with females that laid larger clutches, and that they fledged more young. Furthermore, I found that males with larger Area Flags had lower ectoparasite loads. There was no relationship between the degree to which females expressed their tails and these measures of quality, performance, and reproductive success (chapter 2).

If the tail is a sexually selected in only the male, why do both sexes have such extraordinary raked-tails? Two hypotheses may account for the evolutionary maintenance of the turquoise-browed motmot's elaborate male and female tail-plumage: the tail functions as a sexually selected character in only the male, and: (1) the female tail is expressed as a non-functional correlated genetic response (Lande, 1980; but see Reeve and Sherman, 1993; Amundsen 2000b); or (2) the female tail confers some

naturally selected benefit (i.e., the tail is utilized for some utilitarian purpose; chapter 3).

Further study is required to establish the adaptive benefits, if any, associated with the maintenance of the elaborate female tail. It may prove relevant that both sexes utilize their racketed-tails in a wag-display, whereby the tail is repeatedly rocked side-to-side, similar to the regular motion of a pendulum, and that the display is performed in the presence of predators (chapter 3). It will be necessary to establish the signal content of the wag-display, and to establish if the wag-display yields naturally selected benefits to both sexes. If the tail is utilized for a utilitarian purpose, this would support the hypothesis (Hyp 2) that the elaborate motmot's plumage functions as a sexually selected character in males, and in addition, functions as a naturally selected character in both sexes.

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CHAPTER 2

FUNCTION OF THE RACKETED-TAIL OF THE TURQUOISE-
BROWED MOTMOT: SEXUAL SELECTION FOR MALE TAILS,
BUT NOT FOR FEMALE TAILS

ABSTRACT

The adaptive benefits associated with elaborate male and female plumage are of great interest because most research has focused on male characters, and has ignored elaborate female characters. Both male and female turquoise-browed motmots are elaborately plumed, with long tails tipped with two large rackets. I investigate the hypotheses that the tail functions as a mate-choice or status signal in one or both sexes by testing the predictions that males and/or females with the largest tails will: (1) be in better phenotypic condition; (2) have greater pairing success; and (3) have greater reproductive success. I also investigate if tail-plumage is related to measures of reproductive performance that underlie fledging success (clutch initiation date, clutch size, hatching success). I found that: (i) males with larger racket-tips (Flags) were in better phenotypic condition (fewer ectoparasites); (ii) males (yearlings only) with the longest denuded rachis (Wires) on the central tail feathers had greater pairing success; and (iii) males with longest Wires fledged more young. Longer Wired males had greater fledging success, in part due to pairing with females who laid larger clutches, and also due to greater hatching success (independent of clutch size). There was no relationship between female tail-plumage and measures of condition, pairing success, fledgling success, or reproductive performance. These results support the

hypothesis that tail-plumage functions as a mate-choice or status signal in males, but not in females. I present a hypothesis for the evolutionary maintenance of the elaborate female tail.

INTRODUCTION

Sexual selection generally operates more strongly on males than on females, resulting in greater elaboration of secondary sexual characters among males. However, there are many avian species in which females are also elaborately plumed, and the selective forces that maintain such elaborate male and female characters are of great interest (Amundsen, 2000a). Although researchers have found strong empirical support for the fitness benefits associated with male ornamentation (reviewed in Andersson, 1994), the benefits associated with elaborate female characters are unclear (Amundsen, 2000b).

Five hypotheses have been proposed to explain the maintenance of elaborate characters in both sexes. (Hyp. 1) Elaborate male and female characters can function as mate-choice or status signals used during competition for mates (mutual sexual selection hypothesis; Jones and Hunter, 1993), whereby the most ornamented individuals are of highest quality and are more successful in obtaining higher mating success. The mutual sexual selection hypothesis has been supported by data indicating that elaborate characters are related to male and female: mate preference (Hill, 2002), pairing success (Daunt et al., 2003), reproductive success (Massaro et al., 2003), and to individual quality: phenotypic condition (Velando et al., 2001), survival (Hörak et al., 2001), and dominance (Kraaijeveld et al., 2004). The hypothesis has also been supported by data

indicating assortative pairing for elaborate characters (Andersson et al., 1998; Jawor, 2003; Safran and McGraw, 2004).

(Hyp. 2) Elaborate male and female characters can function as status signals used in intraspecific competition for non-mate resources (social selection hypothesis; West-Eberhard, 1979; 1983). Unlike status signals that function during competition for mates, socially selected status signals function during both intra- and intersexual competition in non-breeding contests for access to territories, foraging sites, or other resources. The social selection hypothesis has been supported by correlative data that has linked elaborate ornamentation to territorial defense by females (Bleiweiss, 1992; Irwin, 1994).

(Hyp. 3) Elaborate male and female characters can function as naturally selected characters used for purposes other than mate-choice or status signals (natural selection hypothesis). Natural selection can exert similar forces on both sexes (Darwin, 1859) and can favor elaborate characters that serve a myriad of utilitarian purposes. For example, elaborate male and female characters can function as: aerodynamic structures that aid in flight (Balmford et al., 1993); signals of toxicity to predators through aposematic warning coloration (Dumbacher et al., 1992), signals that advertise unprofitability to predators (Baker and Parker, 1979), signals that startle prey to facilitate foraging (Mumme, 2002), signals that distract predators from nests (Deane, 1944), signals that disorient predators during attack (Palleroni et al., 2005), signals that deter predator pursuit (Woodland et al., 1980).

Alternatively, elaborate plumage characters can be sexually- or socially-selected in only males, and are: (Hyp. 4) expressed in females as

genetic byproducts due to genetic correlation between the sexes (Lande, 1980; Lande, 1987). This mechanistic model is expandable into a functional hypothesis, which proposes that elaborate female characters are expressed without associated adaptive benefits, and are therefore non-functional (genetic correlation hypothesis), or (Hyp. 5) expressed in females because there is an additional, naturally selected benefit associated with elaborate male and female plumage (combined social- or sexual selection with natural selection hypothesis).

The turquoise-browed motmot is an excellent study organism for an investigation into the function of elaborate male and female plumage. Both sexes are elaborately plumed with long tails --comprising approximately sixty percent of the total body length-- that terminate in large blue-and-black rackets. The distinct racketed-tail typifies the Momotidae, and the turquoise-browed motmot's tail is the most elaborate among the ten species within the family (Forshaw and Cooper, 1987; Snow, 2001; Skutch, 1947), with (1) the longest region of bare rachis ("Wire") on the two racketed tail-feathers, which are denuded for almost half the feather's length, and, (2) the largest oval tips ("Flags") to the racketed feathers, whose vanes are over twice the width of the vanes on the more proximal base of the same feather. Although Darwin (1871, edition 2, p. 404) spoke of the possible ornamental value of the 'spoon-like' tail of the turquoise-browed motmot in his discussion of sexually selected decorations, the signal value of the motmot's unique tail has not been investigated.

I (chapter 1) investigated the function of the motmot's elaborate tail by testing if pairs form assortatively for tail-plumage. I found that pairs

do not form assortatively, and concluded that the male and female tail-plumage is not a sexually-selected character in both sexes. However, I demonstrated that the Wire and Flag of the tail were larger in males than in females, and that the tail-plumage was expressed with a high degree of variation. Based on these observations, I suggested that the turquoise-browed motmot's racketed-tail functions as a sexually- or socially-selected character in males, but not in females.

Here I further test if the elaborate male and female tail of the turquoise-browed motmot functions as a sexually- or socially-selected character in one, or in both sexes. Specifically, I test the predictions that males and/or females with the largest tail-plumage will: (1) be in greater phenotypic condition; (2) have greater success at acquiring a mate (pairing success); and (3) fledge more young. I also investigate if tail-plumage is related to measures of reproductive performance that may underlie reproductive success (clutch initiation date, clutch size, and hatching success).

MATERIALS AND METHODS

Study organism and study site

I studied the turquoise-browed motmot (*Eumomota superciliosa*) in the tropical-deciduous thorn-scrub forest located near the Ria Lagartos Biosphere Reserve in northern Yucatan, Mexico (21° 33' N, 88° 05' W) from March to August in 1999-2002. The area is characterized by a six-month wet-dry cycle. The forests in northern Yucatan are relatively devoid of insects during the dry period, and then experience a dramatic

increase in insect biomass when the rainy season begins (Orejuela, 1975). The turquoise-browed motmot is primarily an insectivore (Orejuela, 1980), and initiates breeding at the onset of the rainy season (May-June).

The turquoise-browed motmot breeds colonially, and the species nests in tunnels dug in earthen banks (mean depth = 1.27 ± 0.40 (sd) m) in sinkholes, limestone quarries, freshwater wells, and ancient man-made structures (e.g. Maya ruins; Scott and Martin, 1986). During the breeding seasons (March-August) of 1999-2002, I studied motmots at four colonies located in abandoned limestone quarries (range = 7 - 39 pairs). All breeding colonies were located within a 10 sq km area near the Ria Lagartos Biosphere Reserve, in Northern Yucatan, Mexico ($21^{\circ} 33' \text{ N}$, $88^{\circ} 05' \text{ W}$). The area is characterized by thorn-scrub forest and grazing pastureland and experiences a long dry season (December-May).

The turquoise-browed motmot is socially monogamous, and both males and females incubate and brood, although only females do so at night. Both sexes provision the highly dependent altricial chicks (clutch size: mean = 4.0 ± 0.6 (sd), range 3-5, $n = 78$ nests; nestling period (days): mean = 32 ± 2.9 (sd), range 27-41, $n = 78$ nests), and parental care continues for a 4-6 week post-fledgling period (Skutch, 1947). Pairs fledge a maximum of one brood per year.

In the northern Yucatan, the turquoise-browed motmot is migratory. Both males and females return to the breeding areas at the same time in early March, approximately three months before clutch-initiation. Many pairs arrive at the breeding areas already paired, although pair bonds shuffle as new individuals arrive and compete for nesting territories or partners. Each year, some individuals of both sexes fail to pair and remain as floaters at the

nesting colonies throughout the breeding season. Most unpaired birds are yearlings (see results), which are easily identified by their worn tail-feathers (Chapter 1).

General methods

Each year, motmots were captured with mist nets placed around the colony during a 1.5-month period. Capture efforts began after birds had established pair bonds and nest ownership, and ended before clutch initiation. At each of the four colonies, 95% of all breeders and approximately 85% of floaters were captured and banded with individually recognizable color bands. Because knowledge of individual sex was required while in the field, all birds were sexed by laparotomy. There were no noticeable adverse affects of the procedure: laparotomized individuals were observed behaving normally at breeding colonies the following day.

Behavioral observations were conducted with spotting scopes from within permanent blinds located 45-55m from nesting colonies. To minimize human disturbance, observers entered blinds before sunrise while motmots were away from the colonies on off-colony territories.

Morphological measurements

Morphological measures were taken from all birds in 1999-2002. Linear measures were taken to the nearest 0.1 mm with calipers or with a ruler. Mass was measured with a Pesola scale to the nearest 0.5 g. Tarsus length, bill length, and flattened wing chord length were measured, and values were combined using principal component analysis to compute a

single body-size index (PC1). The first principal component (PC1) explained 53% of the variation in body size. I measured six linear components of the tail (Figure 2.1): 1) Total Tail (central-follicle to the distal tip of the longest central rectrix), 2) Racket (the sum of the Wire (the feather-stem devoid of barbs) and the Flag (the oval shaped tip); 3) Base (central-follicle to the distal tip of the longest second feather -- the tail is graduated, so second feathers are the next longest feathers after the racketed central tail feathers), 4) Wire (the length of rachis devoid of barbs between the distal tip of the Base and the proximal tip of the Flag on the longest central rectrix), 5) Blue of Flag (blue portion of the dorsal surface of the Flag on the longest central rectrix), and 6) Black of Flag (the distal black portion of the dorsal surface of the Flag on the longest central rectrix).

I also measured the surface area of the oval-shaped tip of the largest Flag, herein referred to as 7) Area Flag. In 2002, I photographed feathers using standardized digital photography, and included a size reference. Surface area was later calculated with the ImageJ Software Package (U. S. National Institutes of Health, 1997-2005). I calculated Area Flag for other years by multiplying the length of Flag by its linear width (measured by flattening the Flag with a ruler). The calculated measures were significantly and highly correlated with the measures taken from photographs ($F = 1578.74$, $p < 0.0001$, $r^2 = 83.0$, $n = 324$). Thus, the two types of measures were considered equivalent, and calculated measures were used when photographic measures were unavailable.

Only I collected morphological measurements, and repeatability (the intraclass correlation coefficient) was calculated on a subset of birds

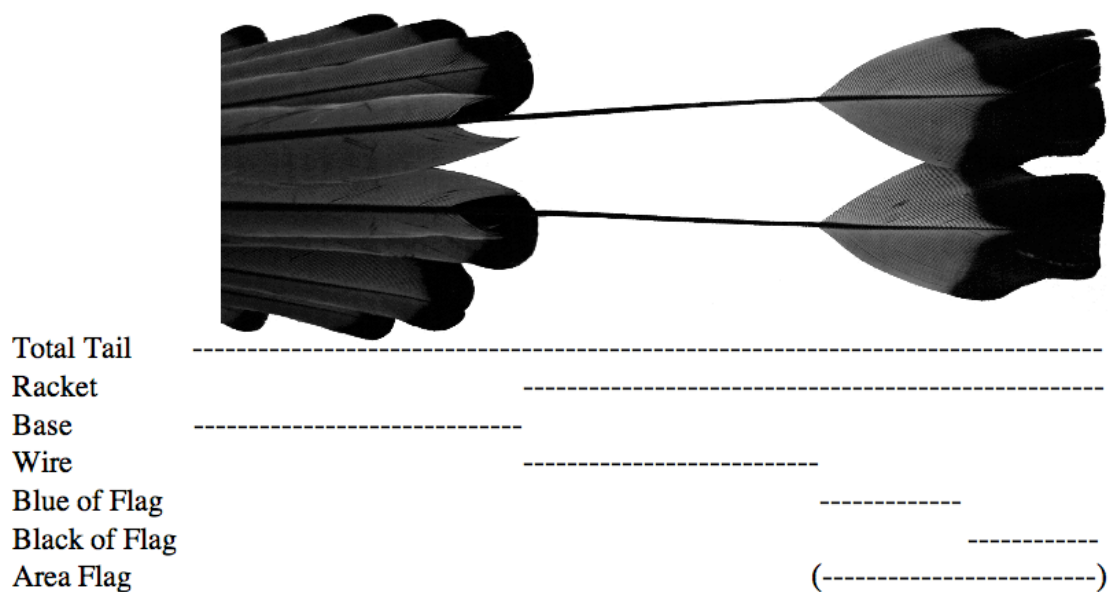


Figure 2.1. Tail-components of the turquoise-browed motmot. The horizontal lines define the linear distance measured for each tail-component. Area Flag was measured as surface-area using standardized digital photography, or by multiplying the Flag's width by its length.

in 2002 by measuring the same individual on different days (after Lessells and Boag, 1987). Repeatability was high for all linear measures of tail-components ($R \geq 0.94$, $n = 15$), and also for surface-area ($R = 0.89$, $n = 15$).

Because body size correlated with the size of many of the tail-components (Chapter 1), I standardized each tail-component for body-size by calculating residual values from regressions of each tail-component on body-size (PC1) (residuals were calculated separately for sexes). Residual values of tail-components were used in all analyses of tail-plumage. To control for potential effects of tail-feather loss on dependent variables, I excluded birds that lost or damaged both central tail-feathers before capture (for analyses on phenotypic condition), or before the initiation of the first clutch of the season (all other analyses). When data from multiple years were combined, only the most recent year's data were used for each individual to avoid pseudoreplication.

Tail-plumage and phenotypic condition

I collected five measures of phenotypic condition from each bird: (i) Size-specific mass. I calculated residuals from the regression of mass on body size to evaluate mass while controlling for skeletal size (Jakob et al., 1996); (ii) Hematocrit. I measured percent erythrocytes in blood samples (year 2002 only). A blood sample was taken from each individual from the brachial vein, and was collected into heparinized microhematocrit capillary tubes. Each tube was centrifuged for seven minutes in a portable centrifuge at 1,500 rpm. Hematocrit was measured as the ratio of blood cell volume to total volume within the capillary tube.

Hematocrit is a widely used serological test to assess a bird's health status (Bush, 1975; Amand, 1986), and can also reflect recent metabolic activity (Palomeque and Planas, 1978; Saino et al, 1997); (iii) Ectoparasite load. Motmots were parasitized by *Philopterus* sp. feather lice (identified with Price et al., 2003). I quantified the degree of *Philopterus* louse infestation by counting eggs, which are laid almost exclusively in the black feathers of the chest-badge (I established that louse eggs are only located in the area of the chest-badge by blowing on body-feathers and visually inspecting the entire body of approximately 200 motmots). To quantify louse load, I exposed eggs by blowing upward on the chest-badge, and counted white eggs along the base of the chest-badge feathers. Each bird received a score of 0 to 5 depending on the degree of infestation; each integer above zero indicated an additional 1-20 eggs (ex. score 2 indicated 21-40 eggs). The majority of adults had some louse-infestation (Males: 97% (161/166) were infested, mean score = 2.4 ± 0.09 ; Females: 93% (136/146) were infested, mean score = 2.5 ± 0.10). *Philopterus* lice have been shown to have a negative effect on their host by reducing feather mass and survival in rock doves (Clayton et al., 1999) and by reducing nutritional condition in magpies (Blanco et al., 2001); (iv) Growth bars. I calculated average growth-bar distance by measuring the distance between 5-7 bars on the blue region of the Flag, and then calculated the mean growth-bar distance from both central tail-feathers (following methods of Grubb, 1989). Growth-bar distance represents the amount of feather growth over a twenty-four hour period, and indicates the amount of energy reserves that were available during molt (Grubb, 1989; 1991); (v) Fluctuating asymmetry. I quantified fluctuating asymmetry as the

absolute value of the difference in length of the two central rectrices.

Body-size was not correlated with asymmetry (male: $F = 0.43$, $p = 0.51$, $n = 48$; female: $F = 0.05$, $p = 0.82$, $n = 52$), so did not bias measures.

Symmetrical growth indicates developmental homeostasis, and individuals with lower phenotypic condition are generally less symmetric (Møller, 1990; Van Valen, 1962).

To test the function of the tail-plumage, I compared the size of adult male and adult female tail-components to four measures of phenotypic condition (size-specific mass, hematocrit, ectoparasite load, and fluctuating asymmetry). The relationship between growth bars and tail-size was not investigated because the daily rate of feather growth is not independent of tail-size (i.e., longer tails arise because more feather is produced per day). Analyses were performed on a combined data set from 2000-2002.

To test if each of the five measures provided similar estimates of an individual's phenotypic condition, I computed intercorrelations among the five measures of phenotypic condition of birds captured in 2002.

Tail-plumage and pairing success

I monitored pairing success of all banded individuals, and classified them as paired or unpaired depending on whether they successfully initiated a clutch together. Because many birds were not seen after initial capture (i.e., they likely moved to other colonies), the category of unpaired birds was restricted to individuals who: (1) were observed throughout the nestling period, and (2) were observed after the date of the last clutch initiation of a newly formed pair. These criteria ensured that birds classified as unpaired

did not breed elsewhere. In 2000 and 2002, 29 birds were excluded because they were not seen after this date.

To test the function of the tail-plumage, I compared the size of adult and yearling male and female tail-components to pairing success. I analyzed pairing success of adults and yearlings separately because there was little variation in adult breeding success (the majority of adults bred each year), whereas out of the large pool of yearlings, only some bred each year (see results). To avoid pseudoreplication, adult pairing success was analyzed separately in year 2000 and 2002 (a manipulative experiment, not reported here, was conducted in 2001). Yearling pairing success was analyzed with combined data from 2000 and 2002, and each yearling was represented only once.

Tail-plumage and fledging success

Adult reproductive success was analyzed in two ways: (1) whether a pair did or did not fledge any young, and (2) how many fledglings were produced from successful nests. Nestlings were determined to have fledged if nestlings survived to 24 days of age. This day was chosen because it is the earliest reported age for fledging in this species (Orejuela, 1977; Scott, 1984).

To test the function of the tail-plumage, I compared the size of adult male and adult female tail-components to these two measures of fledging success. Analyses were performed on a combined data set from 2000-2002.

Tail-plumage and reproductive performance

To quantify clutch-initiation date, clutch size, and hatching success, nest contents were checked every 2-4 days using a lipstick-shaped camera attached to the end of a flexible hose. The camera was illuminated by an infrared light source, and the image was displayed on a small television.

Clutch-initiation date was defined as the date the first egg appeared in the nest. In some cases, the clutch-initiation date was backwards-calculated based on the species-specific 48-hour laying pattern (Scott and Martin, 1983). Because multiple years' data were combined, clutch initiation date was z-score standardized for each year. Clutch size and hatching success were defined as the maximum number of eggs, or nestlings observed within each nest. Because nestlings hatched asynchronously over a 1-5 day period (Scott and Martin, 1986), and because some nestlings died before their younger siblings hatched, I sometimes extrapolated hatching success based on the developmental stage and relative size of chicks within a nest.

To determine the influence of each of these measures of reproductive performance on reproductive success, I correlated these three measures of reproductive performance to each other and to the number of fledglings from each nest. To test the function of the tail-plumage, I compared the size of adult male and adult female tail-components to these measures of reproductive performance. Analyses were performed on a combined data set from 2000-2002, and I analyzed only the primary nesting attempt of each pair because replacement clutches were smaller than primary clutches, and I wanted to evaluate the greatest potential performance of each individual.

Statistics

Correlations among measures of phenotypic condition were investigated with pairwise correlation analysis. General linear models (GLM) were used to investigate the relationship between tail-plumage and phenotypic condition (four models, one for each measure of condition), the number of fledglings, clutch-initiation date, clutch size, and hatching success. Logistic regression models were used to investigate the relationship between tail-plumage and pairing success, and whether individuals fledged any young. Independent variables in all models were: tail-components (Total Tail, Base, Wire, Blue of Flag, Black of Flag, Area Flag), year, and colony. Independent variables were removed one-at-a-time from the model, largest p-values first, until all effects had p-values < 0.15 . When multiple models were performed to address one question, p-values were evaluated after sequential Bonferroni corrections (after Holm, 1979). All models were run separately for the sexes. Adjusted r^2 is reported for all models. Measures of fluctuating asymmetry were log transformed to fulfill assumptions of normality.

All statistical analyses were two tailed, and rejection level was $p > 0.05$. Descriptive statistics are listed as mean \pm standard error, unless otherwise noted as sd (standard deviation). Sample sizes vary between descriptive statistics and analyses on tail-plumage because some banded individuals were observed, but morphological measurements were not available for that year of study.

RESULTS

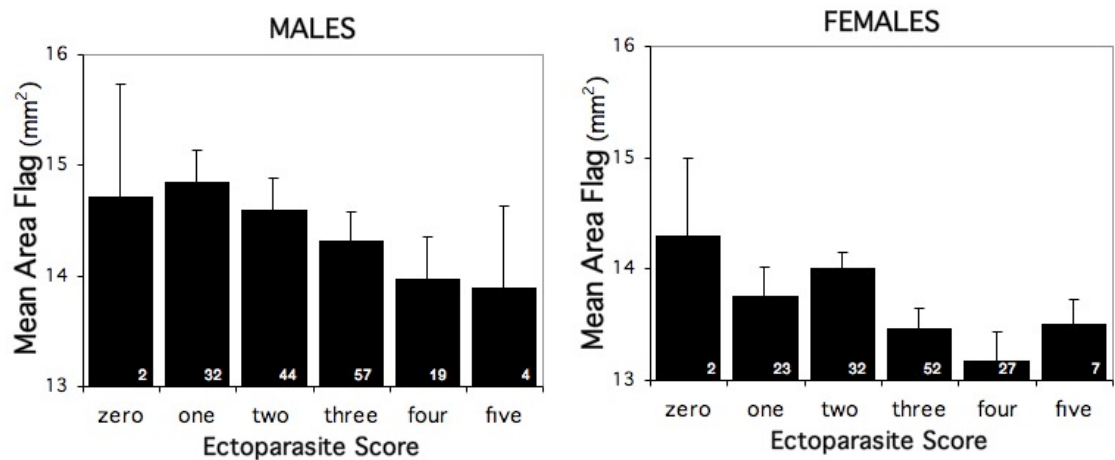
Tail-plumage and phenotypic condition

Ectoparasite score was significantly negatively correlated with male Area Flag (GLM: $F = 12.89$, $p = 0.0004$, $r^2 = 0.16$, $n = 158$), and results were not qualitatively different when the analysis was performed using tail-component values that were not standardized for body-size (Area Flag (GLM: $F = 5.60$, $p = 0.0192$, $r^2 = 0.12$, $n = 158$; Figure 2.2a). However, female tail-components were not significantly correlated with ectoparasite score (sample size: female model = 143; Figure 2.2b: female Area Flag shown for comparison). The three other measures of phenotypic condition (size-specific mass, hematocrit, and fluctuating asymmetry) were not significantly correlated with male or female tail-components (sample sizes: male models = 142-175, female models = 97-150 depending on measure of phenotypic condition). The relationship between male Area Flag and ectoparasite score was significant after sequential Bonferroni correction on multiple tests of condition.

The five measures of each individual's phenotypic condition were not significantly intercorrelated after sequential Bonferroni correction, and correlation coefficients were low (Table 2.1).

Tail-plumage and pairing success

Most of the banded birds that failed to pair at the four colonies were yearlings (yearling unpaired/all unpaired: Male = 69% (20/29), Pearson $X^2 = 4.17$, $p = 0.0411$, $n = 29$; Female = 78% (21/27); Pearson $X^2 = 8.33$, $p = 0.0039$, $n = 27$), and approximately 85% of the un-banded birds that



2.2a

2.2b

Figure 2.2. Relationship between Wire and ectoparasite score for (a) males, and (b) females. Males, but not females, with larger Area Flag had significantly fewer ectoparasites. Ectoparasite score ranges from zero to five, and each positive integer represents an additional 1-20 louse eggs. Sample sizes shown in bottom-right of each bar.

Table 2.1. Product moment correlations between an individual's measures of phenotypic condition (males above, and females below). None of the correlations were significant after sequential Bonferroni correction (sample sizes: males = 126, females = 82).

		Size-specific mass	Hematocrit	Ectoparasite load	Growth-bar	Asymmetry
MALE	Size-specific mass	1				
	Hematocrit	0.02	1			
	Ectoparasite load	-0.08	-0.05	1		
	Growth-bar	-0.08	0.09	0.01	1	
	Asymmetry	0.08	-0.01	0.08	0.15	1
FEMALE	Size-specific mass	1				
	Hematocrit	-0.21	1			
	Ectoparasite load	0.02	0.05	1		
	Growth-bar	-0.06	-0.17	-0.24	1	
	Asymmetry	-0.19	0.21	0.06	0.07	1

were in the unpaired pool of floaters were yearlings. There was a 1:1 sex-ratio of unpaired birds.

Pairing success among yearling males was significantly positively correlated with Wire (Logistic regression: $X^2 = 5.23$, $p = 0.0222$, $r^2 = 0.17$, $n = 25$), and results were not qualitatively different when the analysis was performed using tail-component values that were not standardized for body-size (Logistic regression: $X^2 = 4.49$, $p = 0.0341$, $r^2 = 0.14$, $n = 25$; Figure 2.3a). However, pairing success among yearling females was not significantly correlated with tail-components (sample size: female model = 31; Figure 2.3b: female Wire shown for comparison).

Adult pairing success was not significantly correlated with male or female tail-components (sample sizes: male models = 75 (2002), 36 (2000), female models = 60 (2002), 43 (2000); Figure 2.3c and 2.3d: adult male and female Wire (from 2002) shown for comparison).

Tail-plumage and fledging success

Success at producing at least one fledgling was not significantly correlated with male or female tail-components (sample sizes: male model = 75, female model = 62).

The number of fledglings produced from successful nests was significantly positively correlated with male Wire (GLM: $F = 5.05$, Wire: $p = 0.0062$, $r^2 = 0.29$, $n = 60$), and results were not qualitatively different when the analysis was performed using tail-component values that were not standardized for body-size (GLM: $F = 4.78$, Wire: $p = 0.0044$, $r^2 = 0.27$, $n = 60$; Figure 2.4a). However, female tail-components were not significantly correlated with the number of fledglings from successful

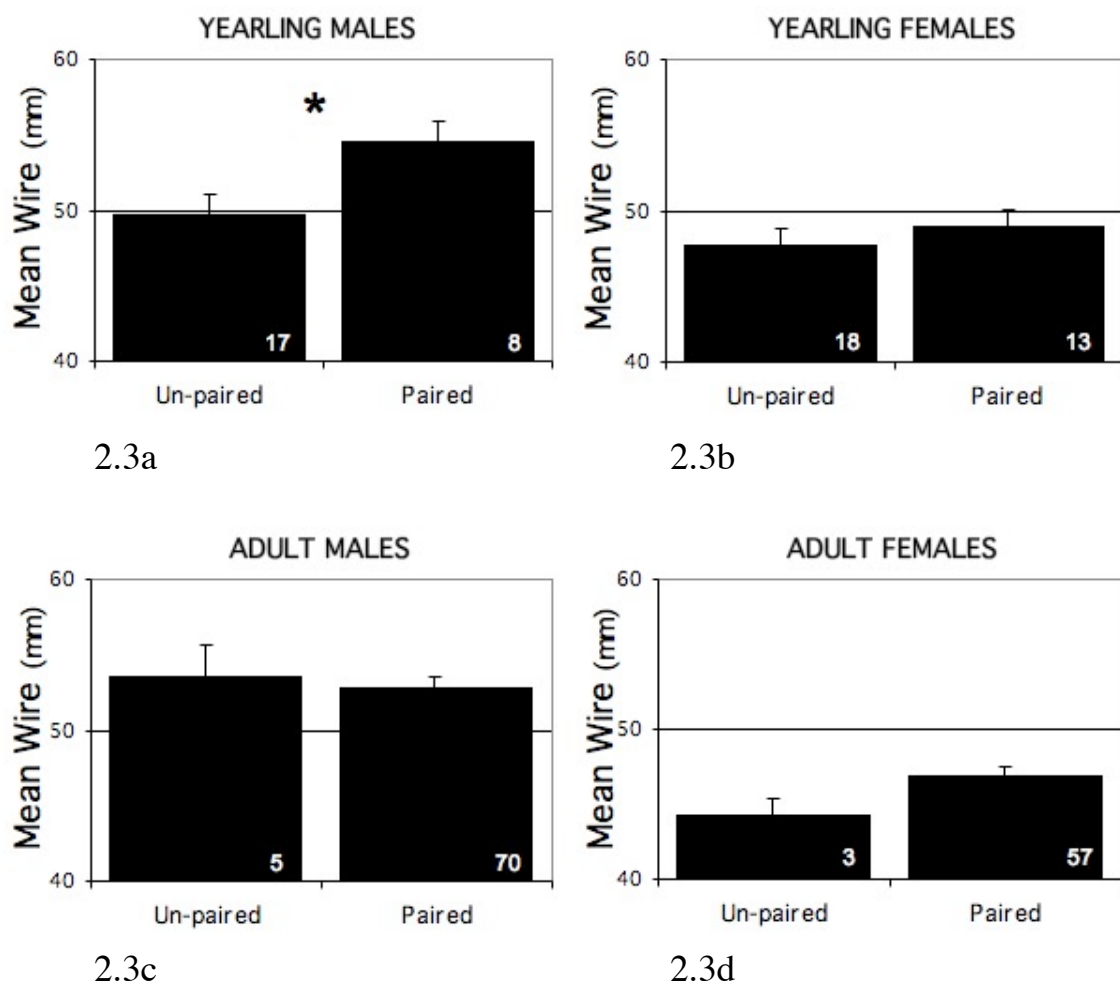
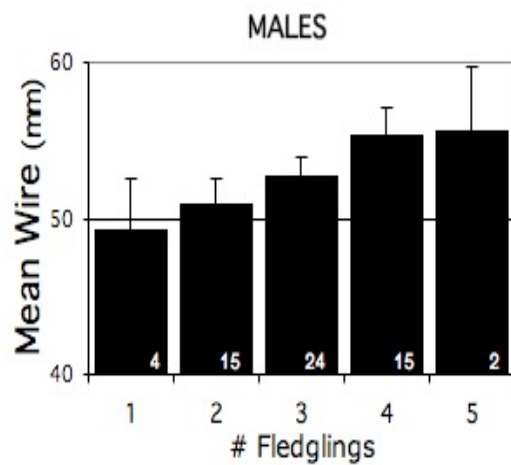
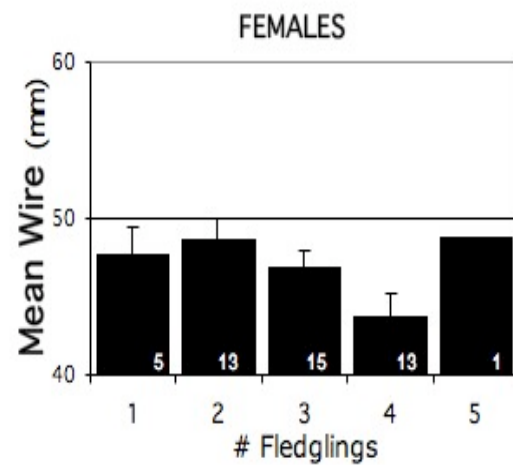


Figure 2.3. Relationship between Wire and pairing success for (a) yearling males, (b) yearling females, (c) adult males, and (d) adult females.

Yearling males, but not females, with longer Wires were significantly more likely to pair. Data on yearlings represents a pooled dataset from 2000 and 2002, and data on adults represent data from 2002 only. Sample sizes shown in bottom-right of each bar.



2.4a



2.4b

Figure 2.4. Relationship between Wire and the number of fledglings from successful nests for (a) males, and (b) females. Males, but not females, with longer Wires fledged significantly more young. Sample sizes shown in bottom-right of each bar.

nests (sample size: female model = 47) (Figure 2.4b: female Wire shown for comparison).

Tail-plumage and reproductive performance

Breeding was synchronous among colonies (first clutch initiated at four colonies within: mean = 4.3 ± 1.5 (sd) days, n = 3 years). Primary clutches were initiated over a four-week period (mean = 29.0 ± 4.0 (sd) days, n = 3 years), although most primary clutches were initiated around the same date early in the season (days into clutch initiation period: mean = 9.9 ± 6.8 (sd), n = 3 years). Clutch size was variable in primary nests (range = 3 - 6, mean = 4.1 ± 0.5 (sd), n = 76), and a least one egg hatched in 76% (58/76) of primary nests (range = 2 - 5, mean = 3.8 ± 0.9 (sd), n = 58). Most pairs successfully produced at least one fledgling after 1-3 nesting attempts (79% (65/82); range = 1 - 5, mean = 2.8 ± 1.0 (sd), n = 65).

Clutch-initiation date (standardized by year and colony) was not significantly correlated with clutch size, hatching success, or fledging success. Clutch size was significantly positively correlated with hatching success, and fledging success; and hatching success was strongly and significantly correlated with fledging success (Table 2.2). P-values for multiple tests were significant after sequential Bonferroni correction.

Clutch-initiation date was not significantly correlated with male or female tail-components (sample sizes: male model = 72, female model = 58).

Clutch size was significantly positively correlated with male Wire (GLM: $F = 8.54$, $p = 0.0048$, $r^2 = 0.12$, n = 66), and results were not

Table 2.2. Product moment correlations between and among measures of adult reproductive performance and reproductive success from 2000-2002. Clutch-initiation has been standardized so that multiple nests and colonies could be compared. Values come from the first nesting attempt of each pair. Significance indicated (*) after sequential Bonferroni correction.

Variable	by Variable	Correlation	n	p	sig
Clutch-initiation date	Clutch size	-0.12	76	0.28	ns
Clutch-initiation date	# Hatch	-0.08	58	0.56	ns
Clutch-initiation date	# Fledglings	-0.08	65	0.54	ns
Clutch size	# Hatch	0.53	58	<.0001	*
Clutch size	# Fledglings	0.35	61	0.0059	*
# Hatch	# Fledglings	0.57	56	<.0001	*

qualitatively different when the analysis was performed using tail-component values that were not standardized for body-size (GLM: $F = 6.33$, $p = 0.0144$, $r^2 = 0.10$, $n = 66$; Figure 2.5a). However, female tail-components were not significantly correlated with clutch size (sample size: female model = 53; Figure 2.5b: female Wire shown for comparison).

Hatching success was significantly positively correlated with male Wire (GLM: $F = 9.66$, $p = 0.0031$, $r^2 = 0.16$, $n = 51$), and results were not qualitatively different when the analysis was performed using tail-component values that were not standardized for body-size (GLM: $F = 10.52$, $p = 0.0021$, $r^2 = 0.18$, $n = 51$; Figure 2.6a). However, female tail-components were not significantly correlated with hatching success (sample size: female model = 39; Figure 2.6b: female Wire shown for comparison). When clutch size was added to the model to control for the effect of egg number on hatching number, male Wire remained a significant predictor of hatching success (GLM: $F = 4.43$, $p < 0.0406$, clutch size: $p < 0.0001$, $r^2 = 0.39$, $n = 51$), yet hatching success (after egg number was controlled) was not significantly correlated with female tail-components.

DISCUSSION

Much research has focused on the signal value of elongated avian tails (Andersson, 1992; Fitzpatrick, 1998) because long tails are thought to handicap normal aerodynamic function (Balmford et al., 1993). Relatively little research, however, has focused on long tails when expressed in both sexes (for exceptions see: Bolland et al., 2004; Cuervo

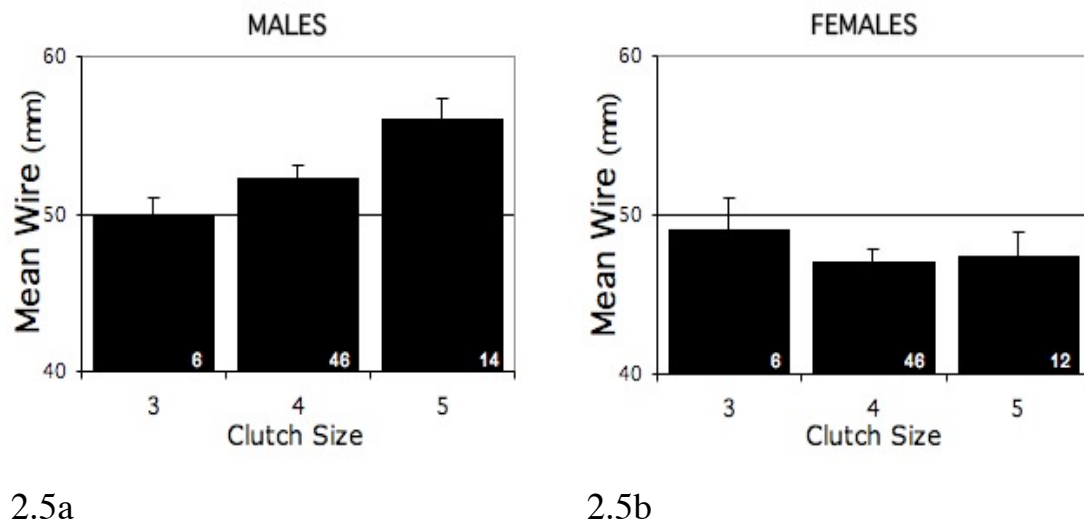
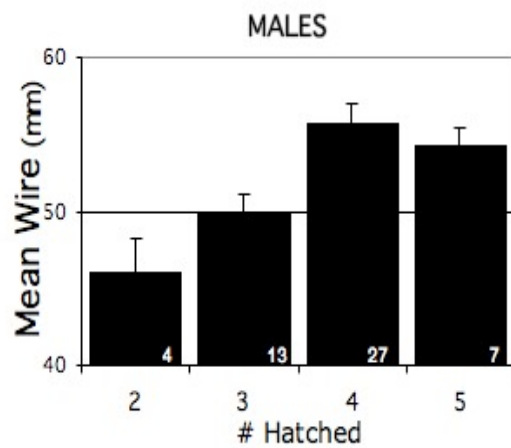
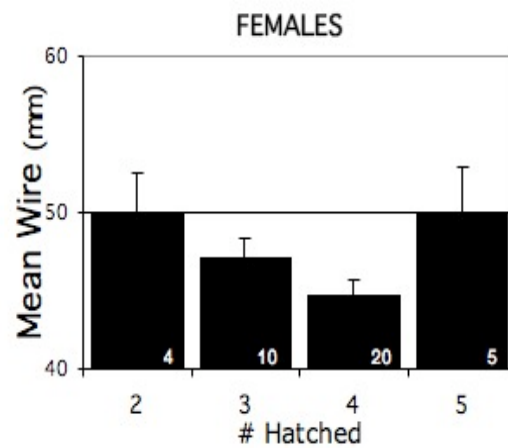


Figure 2.5. Relationship between Wire and clutch size for (a) males, and (b) females. Males with longer Wires paired with females that laid significantly larger clutches. There was no significant relationship between female Wire and her clutch size. Sample sizes shown in bottom-right of each bar.



2.6a



2.6b

Figure 2.6. Relationship between Wire and number of eggs that hatch for (a) males, and (b) females. Males, but not females, with longer Wires hatched significantly more young. Sample sizes shown in bottom-right of each bar.

et al., 1996; Møller, 1993; Regosin and Pruett-Jones, 2001; Veit and Jones, 2004), and there is little consensus on whether both males and females accrue an adaptive benefit from elaborate tail-plumage.

Results support the hypothesis that the male tail, but not female tail is a sexually- or socially-selected character. First, among males, but not among females, the Area Flag was positively correlated with lower parasitic infestation of *Philopterus* lice. *Philopterus* lice (Phthiraptera: Ischnocera) feed on feathers, and infestation leads to reduced plumage insulation and an increase in thermoregulatory demands on their hosts, resulting in reduced host body mass (rock doves, Booth et al., 1993) and survivorship (rock doves, Clayton et al., 1999), and by reducing nutritional condition (magpies, Blanco et al., 2001). The negative correlation between parasite load and expression of the male Flag suggests that the Flag may be a condition-dependant indicator of quality. It is likely that the size of a male's Flag reflects an individual's ability to perform general maintenance (sensu, Walther and Clayton, 2005), whereby higher quality individuals incur lower relative costs than low-quality individuals, and are therefore able to invest more energy into feather growth (Zahavi, 1975; Grafen, 1990). General maintenance and parasite removal require a significant amount of time and energy (Cotgreave and Clayton, 1994; Croll and McLaren, 1993) and prevents individuals from spending time performing other essential behaviors such as feeding and vigilance (Redpath, 1988).

Interestingly, male tail-components are not correlated with the other measures of phenotypic condition: size-specific mass, hematocrit, or fluctuating asymmetry. Unfortunately, my five measures of phenotypic

condition are not intercorrelated, and thus it is unclear if most of my measures accurately reflect phenotypic condition. The lack of agreement between the different measures of condition could signify that most of my measures are unreliable indicators of an individual's true phenotypic condition.

Second, among yearling birds, male but not female Wire was positively correlated with pairing success. The mean length of Wire among yearling males that successfully acquired a mate is similar to the mean length of Wires of adult males, and this may indicate that there is a minimal Wire-length, below which, a male is very unlikely to gain access to a mate. Although there is no relationship between pairing success and tail-components among adults, this could be explained because so few adults failed to pair, and the extremely small variance in adult pairing success limited statistical power. With a more extensive sampling, there may have been a detectable difference in tail-components between adults that paired, and those who did not.

Third, males but not females with longer Wires fledged more young in successful nests. The higher fledgling success of longer Wired males is explained in part by two aspects of reproductive performance: (1) males with longer Wires pair with females who lay larger clutches, and (2) males with longer Wires hatch more young, and do so independent of clutch size. These relationships may arise because males with longer Wires: (i) gain access to females which are of higher quality and are thus able to lay larger clutches, lay higher quality eggs, or invest more into incubation; (ii) gain access to females that invest more into reproduction because they are paired to a high-quality male (Burley, 1986). If either of these mechanisms account for the

greater fledgling success of long Wired males, this would be consistent with the Darwin-Fisher mechanism of sexual selection in monogamous species (Darwin, 1871; Fisher, 1958; Kirkpatrick et al., 1990), whereby more ornamented males gain a selective advantage by pairing with females with greater reproductive success (O'Donald, 1980; Møller, 1994). It is also possible that sexual selection acts more strongly on males because males with longer Wires increase their mating success through extra-pair fertilizations. Further study is necessary to assess the occurrence of extra-pair fertilizations in this species.

The positive relationship between hatching success and male Wire may arise because males with longer Wires are of higher quality and invest more into incubation, or because they give rise to more viable eggs.

In addition to sexual selection explanations, the positive relationship between male Wire and reproductive success could arise if the male Wire functions as a socially-selected status signal used during intraspecific competition for access to non-mate resources. Males with longer Wires could secure access to better resources for themselves and their mates (i.e., possibly better foraging territories), allowing them to invest more into clutch size, egg quality, or parental care.

The greater pairing success and fledgling success of long Wired males strongly supports the hypothesis that the male tail-plumage is subject to directional sexual selection, and also possibly social-selection. It is interesting that a different tail-component, Area Flag, is correlated to phenotypic condition, but not correlated with my measures of reproductive success, and likewise it is interesting that Wire is correlated with reproductive success, but not with my measures of phenotypic

condition. One way to explain this discrepancy is to regard the Area Flag and Wire as separate ornaments. Møller & Pomiankowski (1993) proposed two functions to multiple ornaments: (1) Multiple messages--each ornament reflects a discrete aspect of individual quality; and (2) Redundant signals--all ornaments reflect overall individual quality. I propose a multiple message function to the different components of the tail, whereby the Area Flag indicates ectoparasite load, and I suggest that it is possible that Wire relates to some unmeasured aspect of phenotypic condition, or that the relationship between wire and phenotypic condition was not detected due to the unreliability of many of my measures of phenotypic condition.

The evidence I presented supports the hypothesis that the racketed tail of the male is a sexually- and possibly also a socially-selected character; however, the question remains: why do females also express the elaborate racketed-tail? Other research has also found benefits associated with male, but not with female characters (Hill 1993; Cuervo, 1996; Muma and Weatherhead, 1989; Wolf et al., 2004), and these studies concluded that the genetic correlation hypothesis, which was the null, was likely to account for what they argued were non-functional elaborate female characters (but see Hill, 2002 for updated results).

The genetic correlation hypothesis proposes that elaborate female characters are non-functional. Thus, the hypothesis can be rejected by demonstrating an adaptive function to female characters. In previous work (chapter 3), I showed that both males and females gain a naturally selected benefit from the racketed-tail. I presented evidence that the tail is utilized by both sexes in a wag-display, whereby the tail is repeatedly

rocked side-to-side in a pendulous fashion, and I argued that the racketed-tip and the length of the tail amplify the signal. I supported the pursuit-deterrent signal hypothesis by demonstrating that the wag-display is performed: (i) when motmots detect predators, (ii) in the absence of conspecifics, and (iii) in the same manner irrespective of the presence of potential conspecific receivers. Because female turquoise-browed motmots gain a naturally selected benefit by using their racketed tail in the wag-display, the genetic correlation hypothesis can be rejected. Furthermore, the use of the tail in the wag-display supports hypothesis that natural selection maintains the male and female tail-plumage for pursuit-deterrent signaling, and that sexual- and possibly also a social-selection selects for even more elaborate male tail-plumage. The moderate sexual dimorphism in the turquoise-browed motmot's Wire and Area Flag (chapter 1) further support this hypothesis.

There are two lines of evidence argue against the general explanatory power of genetic correlation hypothesis. (1) In species where elaborate characters are expressed with only moderate sexual dimorphism, the genetic correlation hypothesis is unlikely to apply because sexually selected male ornaments are generally costly to produce or maintain in order to ensure signal honesty (Bradbury and Vehrencamp, 1998), and females would not be selected to produce or maintain a costly form of the 'male-like' character without an associated benefit (Amundsen, 2000b, Reeve and Sherman, 1993; 2002, Sherman and Westneat, 1988). (2) Comparative data have demonstrated that genetic constraints do not appear to inhibit the loss or gain of dimorphism (Price and Birch, 1996). Specifically, it has been shown that over evolutionary history, elaborate characters in one sex change

independently of the direction of change in the other sex (Figuerola and Green, 2000), and that changes in characters from drab to colorful (and in the other direction) have occurred much more frequently in females than in males (Irwin, 1994; Burns, 1998). The direction of the latter result strongly contradicts the genetic correlation hypothesis.

The combined effects of natural selection for elaborate male and female characters, and sexual- or social-selection for further male elaboration may occur in many species with elaborate males and females. For example, in the barn swallow, males have elongated tail streamers that are used to attract mates, and females gain no sexually selected benefits from the expression of ‘male-like’ tails (Møller et al., 1998). Female barn swallows, however, utilize their tails for aerodynamic maneuverability, and the mean female tail-streamer length is at a naturally selected optimum to aid in aerodynamic lift (Hedenström, 1995). In African antelope, males have long horns that function during intersexual competition for access to mates, and females gain no sexually selected benefits from the expression of smaller ‘male-like’ horns (Geist, 1966). Female antelope, however, use their horns to drive predators away from their offspring (Packer, 1983). These examples are very similar to what I believe is occurring with the motmot’s tail: males gain a sexually- and possibly also a socially-selected benefit from their long racketed-tails, and females gain a naturally selected benefit (which they share with the male) by deterring predator pursuit by wag-displaying with their long racketed-tail.

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CHAPTER 3
PREDATOR-ELICITED VISUAL SIGNAL: WHY THE TURQUOISE-
BROWED MOTMOT WAG-DISPLAYS ITS RACKETED TAIL

ABSTRACT

Both sexes of the turquoise-browed motmot (*Eumomota superciliosa*) perform a wag-display, whereby their long racketed-tail is repeatedly rocked side-to-side in a pendulous fashion. The wag-display is performed in two contexts: 1) when predators are in the vicinity, and 2) immediately before entering their nest to deliver food to nestlings. The predator-elicited wag-display is performed throughout the year, whereas the pre-feeding wag-display is performed only during the latter part of the breeding season. I investigated the function the wag-displays by testing if the presence of potential receivers (kin, conspecifics, mate) modified the way in which the wag-displays were performed. Three hypotheses addressed the function of the predator-elicited wag-display: pursuit-deterrent signal, warning alarm signal, and self-preservation alarm signal. I found that the predator-elicited wag-display was performed by motmots who were: (1) alone, and not within signaling distance of conspecifics, (2) unpaired, and therefore not signaling to a mate, and (3) paired, but away from their mate. Motmots in these contexts performed the wag-display with the similar probability, and in a similar manner as: (1) birds that were within signaling distance of conspecifics, (2) paired birds, (3) paired birds who were near their mate. These results support the hypothesis that the predator-elicited wag-display is oriented to the predator, and functions as a pursuit-deterrent signal. The pre-feeding wag-display was performed

prior to only 20% of food-deliveries, and was performed in the absence of predators. I discuss the possibility that the pre-feeding wag-display also functions as a pursuit-deterrent signal, and is performed in this context due to a lowered response threshold due to an increased risk of predation when nestlings are being fed.

INTRODUCTION

Many species of birds display elaborate tail-plumage, and the signal value of such displays has received much attention (Fitzpatrick, 1998). For example, the peacock (*Pavo cristatus*) fans its train while displaying in a lek (Petrie et al., 1991), the slate-throated redstart (*Myioborus miniatus*) spreads its tail to flush insects (Mumme, 2002), and the eastern swamphen (*Porphyrio porphyrio* L.) flicks its tail to deter predators from pursuit (Woodland et al., 1980). The turquoise-browed motmot (*Eumomota superciliosa*) displays its tail in an exaggerated fashion, with a side-to-side movement of the tail similar to the regular motion of a pendulum, but the signal value of the motmot's wag-display is unknown (Snow, 2001). During the motmot's wag-display, the tail is first cocked to approximately 50 degrees to one side of the body, where it pauses briefly before being swung to the other side, in total describing an arc of approximately 100 degrees. The side-to-side motion is repeated many times during a display, and due to the recurring nature of the wag-display, the tail movement commonly draws attention to an otherwise hidden bird. Indeed, nearly 100 years ago, Beebe (1910) noted, "It would be thoroughly protected on its perch among green foliage were it not for the constant and violent jerking of the closed tail from side to side... This

movement, accentuated by the large isolated rackets, calls instant attention to the bird as one looks in its direction”.

The central two tail feathers are long in both sexes, comprising approximately sixty percent of the overall length of the bird, and they are strikingly patterned blue and black (chapter 1). There are two large rackets at the tip of the tail, which appear to hang, unattached, below the rest of the tail. The apparent detachment is caused by the wearing off of weakly attached vanes along the rachis of the two elongate central rectrices (Beebe, 1910). The vanes of the tip of the racket are substantially wider than the other vanes on the same feather (Figure 3.1), which, in combination with the denuded feather shaft and striking coloration, augments the optical effects of the tail movements (Sick, 1985).

The adaptive function of the wag-display has been conjectured, but has not yet been systematically investigated. Wagner (1950) noted that motmots invariably kept their tails still when unaware of his presence, and then began the wag-display as soon as he attracted their attention, suggesting an antipredator function for the display. Likewise, Snow (2001) speculated that the wag-display serves some communicative function, while others have suggested cognitive mechanisms underlying the display including ‘excitement’ (Skutch, 1964), ‘alarm’ (Smith, 1983), ‘uneasiness’ (Fjeldså and Krabbe, 1990), and ‘disturbance’ (Ridgley and Greenfield, 2001).

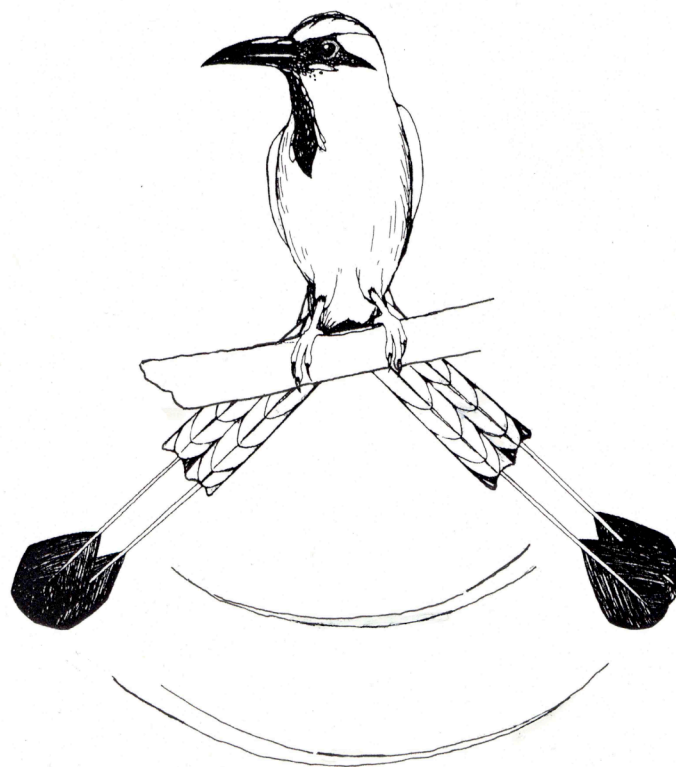


Figure 3.1. Wag-display of the turquoise-browed motmot's racket-tipped tail.

Predator-elicited Wag-display

Based on previous reports and my own observations that the wag-display is performed in the presence of predators, I propose three non-mutually exclusive adaptive hypotheses to address the function of the wag-display (Table 3.1). These hypotheses fall into two categories based on the potential receivers of the signal: predators or conspecifics.

The first hypothesis proposes that the predator-elicited wag-display is directed toward the predator, and functions as: (Hyp1) a pursuit-deterrent signal. A pursuit-deterrent signal is a form of interspecific communication between prey and predator, whereby the prey indicates to a predator that pursuit would be unprofitable because the signaler is prepared to escape (Woodland et al., 1980). Pursuit-deterrent signals fall into two categories; they can advertise prey's ability to escape, and reflect phenotypic condition (quality advertisement) (Zahavi, 1977; Hasson, 1991), or they can advertise that the prey has detected the predator (perception advertisement; Woodland et al., 1980). Pursuit-deterrent signals provide a benefit to the signaler and to the receiver; they prevent the sender from wasting time and energy fleeing, and they prevent the receiver from investing in a costly pursuit that is unlikely to result in capture. Such interspecific signals are typically given at safe distances from predators and are reserved for predator species that stalk or course after their prey. Species that attack with great speeds, such as birds of prey, or predators that are not detected until they are close enough to be of immediate danger, typically do not elicit these displays (Hasson, 1991). Pursuit-deterrent signals have been reported for a wide variety of taxa, including fish (Godin and Davis, 1995), lizards (Cooper et al., 2004),

Table 3.1. Three hypotheses and corresponding predictions address the function of the predator-elicited wag-display. ‘Y’ or ‘N’ describes the direction of the prediction under each hypothesis.

		Hypotheses		
		HYP 1	HYP 2	HYP 3
Predictions		Pursuit-deterrent Signal	Warning Alarm Signal	Self-preservation Alarm Signal
	Display performed in absence of conspecifics	Y	N	N
	Display modulated by presence of conspecifics	N	Y	Y
	Display modulated by presence of mate	N	Y	N
	Display only performed by mated individuals	N	Y	N
	Conspecifics move toward each other	N	N	Y
	Conspecifics move toward predator	N	N	Y

ungulates (Caro, 1995), rabbits (Holley, 1993), primates (Zuberbühler et al., 1997), and birds (Alvarez, 1993). If the motmot's wag-display functions as a pursuit-deterrent signal, and the predator is the intended receiver, the hypothesis predicts that when a predator presents a threat: (i) the wag-display will be performed in the presence of conspecifics, but will also be performed in the absence of conspecifics, and (ii) that the wag-display will not vary in the way it is performed when conspecifics are present or absent.

Alternatively, the motmot's predator-elicited wag-display may be directed toward conspecifics, and functions as: (Hyp2) an alarm signal that warns conspecifics (warning alarm signal). If so, it could protect kin, conspecifics, or the mate from predation, and would benefit the signaler if the receivers are related (Hamilton, 1964), if they reciprocate (Trivers, 1971), or if the receiver is a mate (Morton and Shalter, 1977). If the motmot's wag-display functions as warning alarm signal, the hypothesis predicts that when a predator presents a threat: (i) the wag-display will be performed only when appropriate conspecific receivers are present (Caro, 1986), and not performed in the absence of conspecifics. Note that in regards to the presence of conspecifics, the direction of this prediction is opposite that of Hyp1. This hypothesis also predicts that: (ii) if the mate is the intended receiver (i.e., if other potential receivers are excluded as possibilities), unpaired birds should not perform the wag-display. Such receiver discrimination occurs in many social species (Blumstein et al., 1997; Griesser and Ekman, 2004; Hoogland, 1983; Hoogland, 1996; Sullivan, 1985), and in some cases, alarm signals are modulated

depending on the degree of relatedness between the sender and particular receivers (Sherman, 1977; 1985).

The third possibility is that the wag-display is directed toward conspecifics, but functions as: (Hyp3) an alarm signal that reduces the signaler's predation risk (self-preservation alarm signal). A signaler's predation risk can be reduced if conspecifics group around the signaler (Cresswell, 1994a; Hamilton, 1971), if conspecific receivers mob the predator (Curio, 1978), or if conspecific receivers are manipulated into fleeing toward the predator (Charnov and Krebs, 1975). If the wag-display functions as an alarm signal that reduces the signaler's predation risk, the hypothesis predicts that the wag-display will be performed when a predator presents a threat, and: (i) that conspecifics will react to the wag-display by moving closer together to reduce the signaler's immediate risk of being preyed upon (group), or (ii) that conspecifics will move closer to the predator (mob, or flee toward predator).

I tested among these three hypotheses, by recording the responses of motmots when they encountered natural predators, and when they were experimentally presented with a feral cat and a human. I investigated whether the presence or absence of potential receivers affected the probability of performing the predator-elicited wag-display, or the manner in which the display was performed.

Pre-feeding Wag-display

During a short (4 week) period of the breeding cycle, motmots occasionally perform the wag-display in a second context: immediately before they deliver food to nestlings. Such pre-feeding wag-displays are

performed before approximately 20% of feedings, and performed by both sexes in the absence of apparent predators. I propose three non-mutually exclusive adaptive hypotheses to test whether the pre-feeding wag-display functions differently from the predator-elicited wag-display. The hypotheses fall into two categories based on the intended recipient of the signal: conspecifics or predator.

The pre-feeding wag-display may be directed toward conspecifics, and function as: (Hyp1) a signal to alert nestlings to food delivery. This type of signal is predicted to be performed in front of the nest where it would be detectable by nestlings. Another possibility is that the pre-feeding wag-display is directed toward conspecifics, and functions as: (Hyp2) a signal to draw attention to food in the signaler's bill in order to advertise parental quality to prospective mates. This type of signal is predicted to be performed more often, or performed with greater intensity when: (i) the size of captured prey is large, and (ii) the mate is present. Alternatively, the pre-feeding wag-display may be directed toward an unseen predator, and function as: (Hyp3) a pursuit-deterrent signal, performed because the bird is especially vulnerable to predation when making repeated deliveries to the nest.

In order to test among the three hypotheses, I recorded whether the presence or absence of potential receivers affected the probability of performing the pre-feeding wag-display, or the manner in which the display was performed.

MATERIALS AND METHODS

Study organism

The turquoise-browed motmot is a socially monogamous insectivore that nests in tunnels built in earthen banks (0.4 - 2.2 m in depth, mean = 1.3 m). The species breeds colonially in the Yucatan Peninsula, and colonies are located in the walls of sinkholes, fresh-water wells, limestone quarries, and ancient man-made structures (e.g. Maya ruins; Scott and Martin, 1983). Colony size ranges from 2 to 60 pairs, with colonies of 10-20 pairs being most common (Orejuela, 1977). The species is migratory, and pairs arrive at breeding colonies approximately three months before clutch initiation (March). During the pre-laying period, the birds spend mornings at the colony renovating and defending tunnel-nests. After the rainy season begins (May-June), activity levels increase at the colony, and motmots defend nest sites throughout the day. Both males and females incubate, brood, and provision nestlings. Pairs also defend off-colony foraging and roosting territories, located up to 2km from the colony. Pairs forage and roost on off-colony territories throughout the breeding season, except during incubation and early-stage brooding, when the female alone incubates or broods at night.

Study area and general methods

I studied turquoise-browed motmots during the 1999-2002 breeding seasons (March-August) in the thorn-scrub forest near the Ria Lagartos Biosphere Reserve in northern Yucatan, Mexico (21° 33' N, 88° 05' W). I studied four colonies located in abandoned limestone quarries (range 7-39 pairs), and three colonies located in fresh-water wells (approximate

range 20-30 pairs). To facilitate individual identification, individuals were marked with color bands. Approximately 98% of all breeders and approximately 85% of non-breeding floaters were banded. In the final year of study, I observed 488 banded motmots at the seven colonies.

During approximately 9100 observation-hours at seven colonies, my research team collected data on wag-displays when motmots encountered natural predators. In 2002, I experimentally presented a feral cat or a human to motmots at colonies located in limestone quarries. Observations were conducted with spotting scopes from within permanent blinds located 45-55m from the colony. Predator-presentation trials were video taped for later analysis, and monitoring of multiple focal individuals was facilitated by simultaneous recording of behavior by two observers with spotting scopes. To minimize human disturbance, observers entered blinds before sunrise while motmots were away from the colony (likely on their off-colony territories).

Predator-elicited wag-display

Encounters with natural predators

When a potential predator was observed at a colony, I recorded the species and the number of occasions when each type of animal elicited the wag-display. As a separate analysis, I recorded the time between the departure of the animal from the colony and the termination of wag-displays by one focal individual under observation (n = 18 individuals, each on a separate day).

Predator-presentation experiment

The predator-presentation experiment was originally conducted by presenting a feral cat to motmots. Before sunrise, I placed the cat, enclosed within a cage, 10m in front of the colony-face. The cage was divided into two parts: a small compartment was covered with an opaque cloth that prevented the motmots from seeing inside, and this opened into an uncovered larger compartment, via a remote-controlled door. After motmots arrived at the colony in the morning, I collected ten minutes of baseline data. The baseline survey was divided into one-minute intervals, and for each interval, I noted if any birds at the colony performed the wag-display. I then opened the remote-controlled door so that the cat emerged, and continued to collect data for ten minutes. Data were collected in the same way by scoring each minute-interval for the presence or absence of wag-display across the entire colony. I performed the experiment with the cat once, and the reactions of 11 individuals were collected.

Because the feral cat proved difficult to work with, as an alternative, I used a human as a simulated predator. The human emerged from a blind located approximately 80m from the colony, and slowly walked toward the colony-face. Before the human emerged, I collected ten minutes of baseline data by visually scanning the area around the colony, including all trees and perches within 50m of the colony-face. The baseline survey was divided into one-minute intervals, and for each interval, I noted if any motmots at the colony performed the wag-display. In the second half of the experiment, after the human emerged, I continued to collect data in the same way by scoring each minute-interval

for the presence or absence of wag-display by any individuals across the entire colony. I collected data until all birds were flushed away from the colony, or until 10 minutes had elapsed after human-emergence (trial length after emergence of human: mean = 7.7 min, range = 4.0 - 10.0 min). A human was presented 14 times on separate days, and experiments were divided among three colonies. Five human-presentations were made during the pre-breeding season and nine after nestlings hatched. For the latter nine, I collected wag-display data only on individuals who were not delivering food to nestlings (based on the presence of food held exposed in the bill), thus avoiding confounding issues that might arise by monitoring wag-displays when performed in the pre-feeding context.

To see if the wag-display conveys information about immediacy or level of threat, I tested whether the intensity of wagging changed as the human approached the colony. I counted the intensity of wagging (number of side-to-side wags of the tail/minute) performed by one individual per trial, over 10 trials, and correlated the average number of wags with the distance to the approaching human.

Test between hypothesis 1 and 2: Pursuit-deterrent Signal versus Warning Alarm Signal (receivers: kin or conspecifics)

To test the prediction that the wag-display would be performed in the absence of conspecifics, I monitored whether individuals performed the wag-display when a human appeared in three locations where conspecifics (other than the mate) were unlikely to be present: 1) at off-colony territories, where only one pair forages and roosts; 2) at non-colonial nest sites in Yucatan, Mexico, where single nests were separated

by at least 100m; 3) away from the breeding colonies during the non-breeding season (November). In each of these circumstances, I recorded whether the focal bird performed the wag-display when I approached it, and whether potential conspecific receivers were observed. Note that by testing this prediction, I concurrently addressed the hypothesis that the wag-display will only be performed in the presence of kin and conspecifics.

Test of hypothesis 2: Warning Alarm Signal (receiver: mate)

To test if the mate is the likely receiver of the signal, I observed wag-behavior of three categories of birds at the colony during 14 human-presentation trials for a maximum of 10-minutes. First, I determined if unpaired floaters without a mate performed the wag-display. Second, I compared behavior of paired and unpaired birds. Third, I compared behavior of paired birds whose mates were either present or away from the colony. For the latter two comparisons, I compared the probability of performing the wag-display, and the intensity of wagging for each category of bird. Probability of performing the display was computed as the average number of times a wag-display was performed divided by the total number of individuals observed during the experiments. The intensity of wagging was computed as the average number of side-to-side wags of the tail over a one-minute period (standardized for the amount of time each individual was under observation). Data were collected by simultaneously following 1-5 individuals (with a video camera), which were followed for as long as they remained on the colony.

Test of hypotheses 3: Self-preservation Alarm Signal

To determine if motmots react to the wag-display by grouping, mobbing, or fleeing toward a predator, I monitored the reaction of conspecifics to wag-displays during the 14 human-presentation trials. To test if motmots group around the signaler upon detecting the wag-display, I chose two focal birds within a 10 sq m area, and monitored the distance between them just before the human emerged, and then again 2.5 minutes after the human emerged. By waiting two-and-a-half minutes, this ensured that the birds observed the human and any conspecific wag-display, yet was not so long that the focal birds left the colony. In 7 of the trials, both focal birds were at the colony two-and-a-half minutes after the trial begun. To test the hypothesis that the wag-display caused conspecifics to mob or to flee toward the predator, I monitored whether individuals flew toward the human. I randomly chose one individual and monitored it for 10 minutes after the emergence of the predator, noting whether the individual moved, even slightly, toward the human. This procedure was followed for each of the 14 human-presentation trials.

Mot-bot: Wag-display by a robotic motmot

In addition to using the above methods to test if the wag-display is oriented toward conspecifics, I presented to a colony of motmots a robotic motmot (mot-bot) that produced a realistic side-to-side wag-display. The mot-bot was a taxidermic mount outfitted with a magnetic lever attached to the base of the tail. By repeatedly reversing electrical current through the magnet via remote control, I was able to make the tail wag back-and-forth. I presented the mot-bot to motmots five times at three colonies.

Upon detecting the mot-bot's wag-display, birds were predicted to: (i) respond by increasing vigilance, (ii) depart the colony, (iii) perform the wag-display. To measure these variables, I monitored 1-4 individuals located within 5m of the mot-bot for one minute before the artificial wag-display, and for one minute while the mot-bot performed the display. I followed the direction of the gaze of the motmots before and after the mot-bot's wag, and considered birds to have increased vigilance if they scanned the horizon, or directed their gaze away from the colony. I also noted if birds departed the colony, or performed the wag-display.

Pre-feeding Wag-display

General methods

A pre-feeding wag-display was defined as a wag-display performed by a parent with food in its bill when no predator was observed in the vicinity. To establish that no predator was in the vicinity, I visually scanned the colony area and monitored the behavior of other motmots. Because most motmots at a colony typically performed the wag-display when a predator was present, the behavior of non-focal individuals indicated whether a predator was present and visible to motmots

Seasonal increase in occurrence of wag-display: the context of the pre-feeding wag-display

To confirm that the wag-display was performed more often after nestlings hatch, I monitored the behavior of ten pairs early in the breeding season before they had nestlings, and again after they were caring for nestlings. Pairs were monitored for 2 hours, and the survey was divided

into one-minute intervals. I quantified the number of intervals in which a wag-display was observed. To standardize observation times, I used only data from the first 20 minutes each bird was present at the colony.

It is possible that the increase in intensity of wagging was related to the time of year when most birds at the colony had nestlings, and not related to individual nest ontogeny. To separate these possibilities, I observed birds after the first nestlings hatched at the colony, and monitored wag-display of two types of pairs (1) those with nestlings, and (2) those with only eggs in their nest. I monitored pairs for two hours and established whether pairs with or without nestlings were similarly likely to perform at least one wag-display during the first 20 minutes each bird was present at the colony.

Test of hypotheses 1: Alert nestlings to food delivery

To investigate if the wag-display functions to alert nestlings to the arrival of a parent with food, I noted the location of the bird performing the display with food in its bill: directly in front of the colony-face (where nestlings could detect the display), or behind or above the colony-face. I monitored one pair per day for 12 days, and noted the location of each member of the pair during one randomly chosen wag-display during a two-hour observation period.

Test of hypotheses 2: Advertise parental quality

To test prediction (i), that individuals returning to the nest with a large prey item were more likely to perform the wag-display, I first measured prey length and width by comparing the exposed prey to the

length and width of the bill, and used these values to calculate volume of a rectangle ($L \times W^2$). There is little variation in bill size (chapter 1), thus bill size served as a reliable reference with which to measure prey. Next, I monitored feeding events at one nest over a two-hour period, and compared the average prey size of two types of feeding events on the same day at the same nest: deliveries that were preceded by a wag-display, and deliveries that were not preceded by a wag-display. This was repeated at 15 nests, on 15 separate days. I also tested whether individuals wag-displayed more often when the prey they were carrying was large. I randomly selected one pre-feeding wag-display, from 30 individuals (from 15 pairs), and compared prey size to the number of wag-displays (side-to-side wags of the tail) performed. This was repeated at 15 nests, on 15 separate days.

To test prediction (ii), that individuals returning to the nest when their mate was present would be more likely to perform the wag-display, I compared the proportion of feeding events over a two-hour period, of 15 pairs, collected on 15 separate days, that were preceded by a wag display when the mate was either present or absent. I also tested whether the presence of the mate was related to the number of times the wag-display was performed. To establish whether individuals wag-displayed more often when their mate was present, I randomly selected one pre-feeding wag-display when the mate was present and one when the mate was absent from 15 pairs, collected on 15 separate days, and compared prey size to the number of wag-displays (side-to-side wags of the tail) performed in these two scenarios.

Statistics

All tests were run separately for the sexes, but are reported as both sexes combined when significance of the tests were the same for the sexes. Analyses were compared using parametric statistics when assumptions of normality were met, or nonparametric statistics when assumptions were not met. All statistical analyses were two tailed, and acceptance level was set at $p < 0.05$. Descriptive statistics are listed as mean \pm standard error, unless otherwise noted as sd (standard deviation).

RESULTS

Predator-elicited Wag-display

General description

The tail is generally wag-displayed multiple times within a bout, and bouts were generally repeated, after short pauses ($4.7\text{sec} \pm 3.5(\text{sd})$, $n = 20$ individuals), for the entire period a predator (human or natural) was present. The mean number of side-to-side wags within each bout did not differ between the sexes (during human-presentation trials: Male: $4.2 \pm 1.9(\text{sd})$, $n = 21$; Female: $4.5 \pm 2.4(\text{sd})$, $n = 12$; Kruskal-Wallis: $X^2 = 0.01$, $p = 0.91$, $n = 33$), and there was not a significant sexual difference in probability of performing the wag-display (during human-presentation trials: Male: 71% (15/21); Female: 71% (10/14); Fisher's Exact: $p = 0.99$, $n = 35$). At the beginning of most bouts the tail was raised above the head as it simultaneously swung side-to-side, causing the tail to trace a pattern resembling the letter 'Z' on both its upward and downward trajectory.

Most predator-elicited wag-displays (71% (15/21)) were accompanied by a high-amplitude clucking vocalization. The call is

easily localizable due to its high amplitude, because it is repeated, on-and-off for long periods (up to many minutes), and because the call structure has signal-design characteristics of a localizable signal (Figure 3.2), with a full spectrum up to 10 kHz, and a short pulse duration (Bradbury and Vehrencamp, 1998; Klump and Shalter, 1984).

There was not a significant difference in bout length of the predator-elicited wag-display within the breeding season (pre-nestling stage compared to post-nestling stage; Kruskal-Wallis: $X^2 = 0.04$, $p = 0.84$, $n = 32$), or between the breeding and non-breeding seasons (Kruskal-Wallis: $X^2 = 0.28$, $p = 0.60$, $n = 45$).

Encounters with natural predators

Motmots generally performed the wag-display when potential predators approached the colony, but did not wag-display in the presence of every type of animal. Six types of potential predators elicited the wag-display at the colony: (parenthetical values represent occasions when animals did, and did not, elicit the wag-display) feral cats (7, 0), feral dogs (7, 8), Grey Foxes (*Urocyon cinereoargenteus*) (4, 0), Coatimundis (*Nasua narica*) (2, 3), perched birds of prey (17, 5), and humans (>100, 0). All are potential predators on adult motmots and were close enough to see the wag-display being performed. Three other types of potential predators never elicited the wag-display at the colony: snakes (0, 12), Black Iguanas (*Ctenosaura similis*) (0, >100), flying birds of prey (0, >50). Two additional types of non-threatening animals were observed at the colony that never elicited the wag-display, domestic cattle (0, 3), and Eastern Cottontails (*Sylvilagus floridanus*) (0, 7) (Table 3.2).

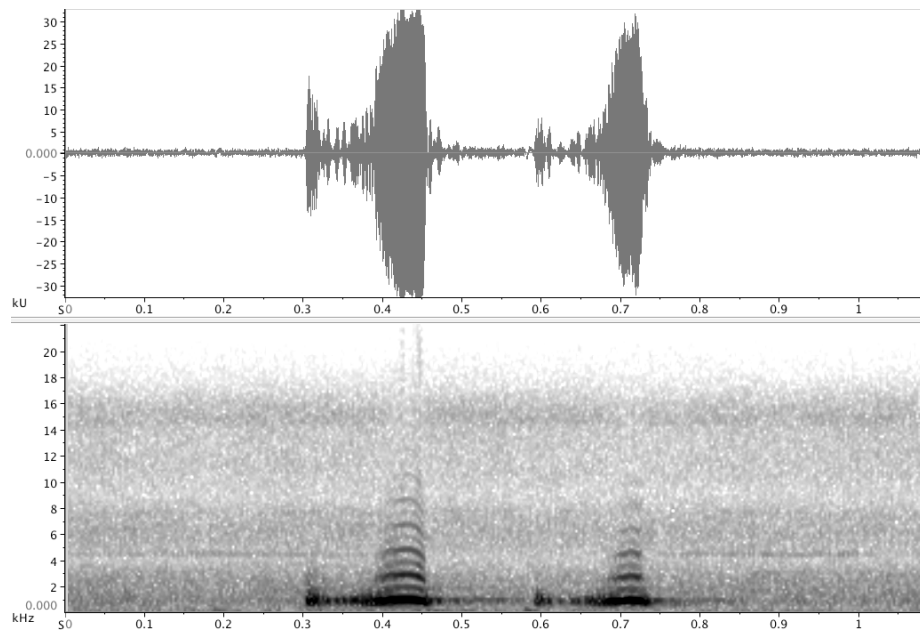


Figure 3.2. The two-part clucking call typically given while a motmot performs the predator-elicited wag-display. The call is typically repeated every few seconds while the bird is performing the wag-display. The call has some signal-design characteristics of a localizable signal, with a full spectrum up to 10 kHz, and a short duration.

Table 3.2. Some animals that approached the colony elicited the wag-display (above), or did not elicit the wag-display (below). The category of animals that did not elicit the wag-display are divided into potential predators, and non-predators. The numbers represent the occasions animals of each category elicited (on left), or did not elicit (on right) a wag-display from at least one individual at the colony.

		Occasions wag-display performed	Occasions wag-display not performed
Did elicit wag-display	Feral Cats	7	0
	Feral Dogs	7	8
	Grey Foxes (<i>Urocyon cinereoargenteus</i>)	4	0
	Coatimundis (<i>Nasua narica</i>)	2	3
	Perched Birds of Prey	17	5
	Humans	>100	0
Did not elicit wag-display	Snakes	0	12
	Black Iguanas (<i>Ctenosaura similis</i>)	0	>100
	Flying Birds of Prey	0	>50
	Domestic Cattle	0	3
	Eastern Cottontails (<i>Sylvilagus floridanus</i>)	0	7

When the potential predators that had elicited the wag-display departed the colony (were out of view from the observer), 72% (13/18) of the focal motmots stopped performing the wag-display within one minute, and the remaining 28% stopped within 3 minutes.

Predator-presentation experiment

There was not a significant difference in the probability of performing the wag-display when presented with a feral cat 73% (8/11 birds) (one experiment), or a human 71% (32/45) (fourteen experiments) (Fisher's Exact: $p = 0.99$, $n = 56$). There also was not a significant difference in the intensity of wagging performed when a feral cat or a human was presented (mean wags/minute: Cat: 9.9 ± 2.2 , $n = 8$; Human: 10.1 ± 1.6 , $n = 32$; Kruskal-Wallis: $X^2 = 0.15$, $p = 0.70$, $n = 40$).

During the 14 human-presentation experiments, motmots rarely performed the wag-display during the ten-minute period before the human emerged from the blind. Throughout the baseline period, motmots performed the wag-display during only 2 of 140 ($< 2\%$) of observation-minutes. The occurrence of wag-display increased dramatically when a human emerged from hiding. Thereafter, at least one motmot performed the wag-display during 73.0% (81/111) of observation-minutes over 14 trials (baseline versus when human visible: Fisher's Exact: $p = 0.99$, $n = 251$; Figure 3.3).

The intensity of wagging (wags/minute) did not significantly change with distance between the human and the focal individual performing the wag-display ($F = 1.69$, $p = 0.23$, $n = 10$).

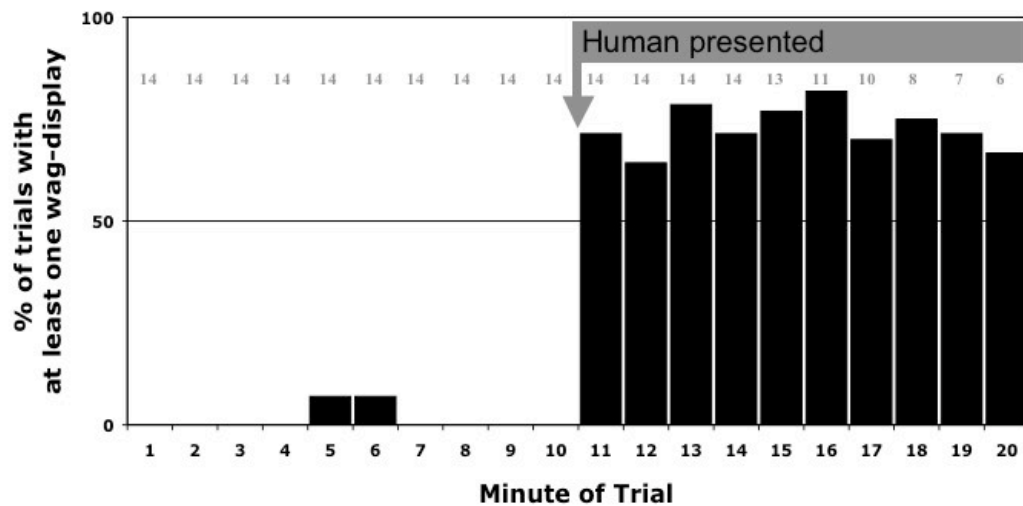


Figure 3.3. The occurrence of wag-display increased when a human was experimentally presented to a colony of motmots. Ten minutes of baseline data were collected before a human emerged from hiding. After minute 10 the human was presented and data were collected for ten minutes, or until all motmots had left the colony. 14 human-presentation trials were conducted. The grey numbers along the top of the graph denote the sample size (number of trials where ≥ 1 bird was at colony) for each one-minute interval.

Test between hypothesis 1 and 2: Pursuit-deterrent Signal versus Warning Alarm Signal (receivers: kin or conspecifics)

When I approached motmots at each of the three locations where they were unlikely to be associating with conspecifics (except possibly the mate), they generally responded by performing the wag-display, and were generally outside of signaling distance of observed conspecifics. At off-colony territories: 87% (27/31) of the individuals who performed the wag-display were not near other observed motmots. At isolated non-colonial nest sites: 100% (10/10) of individuals performed the wag-display when approached, and no other motmots were observed in the vicinity. During the non-breeding season: 75% (12/16) of individuals performed the wag-display when approached, and no other motmots were observed in the vicinity. Thus, motmots wag-display in the absence of apparent conspecific receivers. The probability of performing the wag-display in these three solitary circumstances did not differ significantly from the probability of performing the wag-display during human-presentation trials at the colony (71% 32/45) (Fisher's Exact: $p > 0.05$ in all comparisons).

Test of hypothesis 2: Warning Alarm Signal (receiver: mate)

Unpaired birds

Unpaired birds were observed performing the wag-display during human-presentation trials at the colony; in total seven unpaired individuals performed the wag-display.

Paired versus unpaired birds

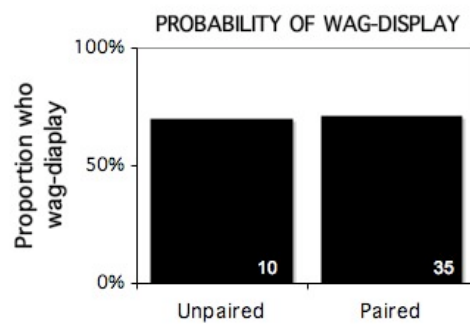
There was not a significant difference in the probability of performing the wag-display by unpaired and paired individuals. During 14 human-presentation trials, 70% (7/10) of unpaired birds performed the wag-display, and 71% (25/35) of paired birds performed the wag-display (Fisher's Exact: $p = 0.99$, $n = 45$; Figure 3.4a). There was not a significant difference in the intensity of wagging performed by unpaired and paired individuals (wags/minute: Unpaired: 12.4 ± 2.7 , $n = 7$; Paired: 9.5 ± 1.9 , $n = 25$; Kruskal Wallis: $X^2 = 2.3319$, $p = 0.1267$, $n = 32$; Figure 3.4b).

Paired and away from mate, versus paired and near mate

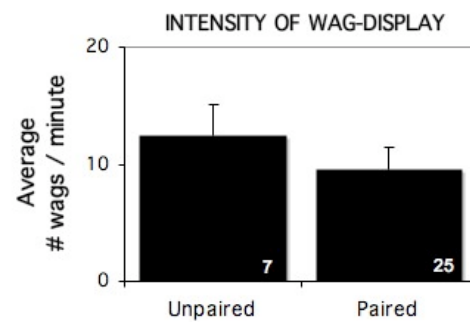
There was not a significant difference in the probability of performing the wag-display by paired birds that were either away from or near their mate: the wag-display was performed by 68% (15/22) of individuals that were away from their mate, and 77% (10/13) of individuals that were near their mate (Fisher's Exact: $p = 0.71$, $n = 35$) (Figure 3.5a). Contrary to the prediction, there was a tendency for paired individuals to wag-display with greater intensity when they were away from their mate (wags/minute: Away from mate: 12.3 ± 2.9 , $n = 15$; near their mate: 5.2 ± 1.3 , $n = 10$; Kruskal Wallis: $X^2 = 2.96$, $p = 0.09$, $n = 25$; Figure 3.5b).

Mot-bot: Wag-display by a robotic motmot

The mot-bot's wag-display did not elicit detectable conspecific responses. Motmots around the mot-bot did not increase vigilance, and only 38% (6/16) changed the orientation of their gaze. In all of these

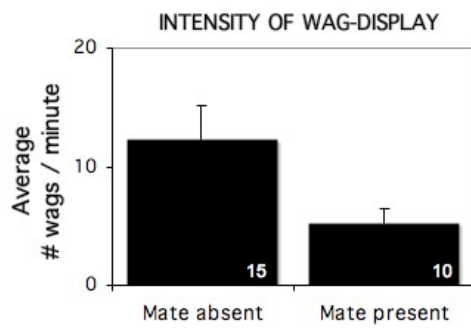


3.4a.

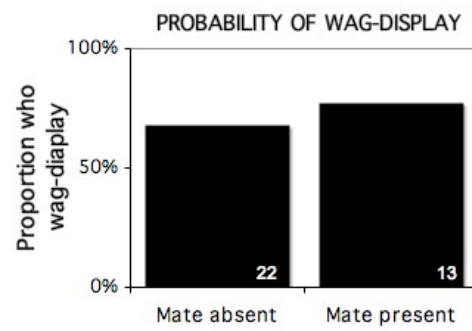


3.4b.

Figure 3.4. When a human was experimentally presented to a colony of motmots, paired status was not related to (a) the probability of performing the wag-display, or (b) the intensity of wagging. Sample size shown in lower right of each bar.



3.5a.



3.5b.

Figure 3.5. When a human was experimentally presented to a colony of motmots, the presence or absence of an individual's mate was not related to (a) the probability of performing the wag-display, or (b) the intensity of wagging. Sample size shown in lower right of each bar.

cases, the birds turned their heads to look at the mot-bot. No birds responded by leaving the colony or performing the wag-display.

Test of hypotheses 3: Self-preservation Alarm Signal

Motmots did not move significantly closer to one another after the appearance of the human (Mean inter-motmot distance one-minute before predator emergence: 3.2 ± 0.91 m; two-and-a-half minutes after predator emergence: 3.4 ± 0.80 m; Wilcoxon Sign-Rank: $p = 0.99$, $n = 7$). They also did not mob, nor did they flee toward the predator during the human-presentation trials: during the ten minutes after the human emerged, the focal motmot either stayed where it was, or moved away from the predator in 93% (13/14) of the trials, and only one individual was observed to move, even slightly, toward the predator 7% (1/14) (Fisher's Exact: $p = 0.99$, $n = 14$).

Pre-feeding Wag-display

General description

The pre-feeding wag-display was performed while a bird sat on a perch within 25m of the nesting colony. The pre-feeding wag-display was performed before food was delivered to nestlings ($n = 76$), but no wag-display was performed after food was delivered ($n = 76$), even though birds frequently returned to the same perch where they had performed the wag-display.

The pre-feeding wag-display was performed prior to only 21% (180/838) of feedings by 38 paired males and females. When delivering food to nestlings, motmots either flew directly into the tunnel-nest without

first landing on a perch located near the colony (30% (257/838) of feedings), or perched within 25m of the nest before entering (70% (587/838) of feedings). When a motmot perched before entering the nest, 31% (180/587) of feedings were preceded by a wag-display.

Not only was the pre-feeding wag-display rare, only 62% (47/76) of focal individuals ever performed the pre-feeding wag-display. Among the 47 birds that performed the wag-display, they only did so prior to 38% (180/478) of feedings. There was not a significant sexual difference in proportion of feedings preceded by a wag display at each nest (Male: mean = 37.0% \pm 21.0sd, n = 25; Female: mean = 42.0% \pm 28.0sd, n = 22; Kruskal-Wallis: $X^2 = 0.12$, p = 0.73, n = 47).

The pre-feeding wag-display was performed in a similar way to the predator-elicited wag-display. During a pre-feeding wag-display, the tail was wag-displayed multiple times within a wag-bout, and bout-length did differ significantly between the sexes (Male: mean = 4.0 \pm 2.1sd, n = 16; Female: mean = 3.4 \pm 1.2sd, n = 14; Kruskal Wallis: $X^2 = 0.24$, p = 0.62, n = 30), and there was not a significant sexual difference in proportion of individuals that were observed to wag-display before feeding chicks (Male: 66% (25/38); Female: 58% (22/38); Fisher's Exact: p = 0.48, n = 76). There was not a significant difference in bout-length between predator-elicited, and pre-feeding wag-displays (Kruskal Wallis: $X^2 = 1.75$, p = 0.19, n = 63). Similar to the predator-elicited wag-display, wag-bouts were generally preceded by an upward and side-to-side "Z" motion of the tail, and wag-bouts were generally repeated, after short pauses, for the entire period before food was delivered to the nest.

A characteristic unique to the pre-feeding wag-display was that the displaying individual carried food in its bill during the display (percent of all wag-displays observed after nestlings hatched by individuals with food in bill = 79% (26/33)). The pre-feeding wag-display was also different in that it was performed without the clucking-vocalization that typically accompanied the predator-elicited wag-display.

Seasonal increase in occurrence of wag-display: the context of the pre-feeding wag-display

Individuals performed the wag-display significantly more often when they were caring for nestlings compared to earlier in the season before nestlings were present (Wilcoxon Sign-Rank: $p < 0.0001$, $n = 20$). Predators were detected by the observer in 100% (3/3) of the cases where wag-display was performed before nestlings hatched, but in only 8% (4/48) of the cases after nestlings hatched.

Individual nesting ontogeny was related to the performance of the wag-display: when nestlings were present, individuals who still had eggs in their nest did not perform the wag-display, whereas individuals with nestlings occasionally performed the wag-display (Percent of surveys where wag-display was observed at least once by either sex: Nest with eggs: 0% (0/6); Nests with nestlings: 73% (16/22) (Fisher's Exact: $p = 0.0025$, $n = 28$).

Test of hypotheses 1, Alert nestlings to food delivery

Pre-feeding wag-displays were rarely performed in front of the colony-face where nestlings could observe the signal (location of pre-feeding wag-display: In front of colony-face = 8.0% (2/24); Behind or

above colony-face = 92% (22/24); Pearson Chi Square: $X^2 = 16.67$, $p < 0.0001$, $n = 24$).

Test of hypotheses 2, Advertise parental quality

There was not a significant relationship between size of prey item delivered to the nest and the probability of performing a pre-feeding wag-display (mean size of prey item during delivery preceded by wag-display = $1531.7 \pm 253.3 \text{ mm}^3$; mean size of prey item during delivery without wag-display = $2583.8 \pm 330.4 \text{ mm}^3$; Wilcoxon Sign-Rank: $p = 0.62$, $n = 30$). There was not a significant relationship between the size of prey item delivered to the nest and the number of wag-displays performed before the parent delivered food to nestlings ($F = 0.72$, $p = 0.40$, $n = 30$).

The presence of an individual's mate was not related to the proportion of feeding events that were preceded by a wag-display (mean proportion of feeding events preceded by wag-display when mate present = $35.0\% \pm 0.09$; when mate absent = $40\% \pm 0.05$; Kruskal-Wallis: $X^2 = 0.63$, $p = 0.43$, $n = 50$), nor to the number of times the tail was wag-displayed before the parent delivered food to nestlings (mean number of wag-displays performed when mate present = 7.3 ± 3.2 ; when mate absent = 9.3 ± 2.2 ; Kruskal-Wallis: $X^2 = 2.53$, $p = 0.12$, $n = 30$).

DISCUSSION

Predator-elicited Wag-display

When the turquoise-browed motmot encounters a predator, it reacts in a predictable and stereotypical manner by performing the wag-display. There are four lines of evidence that link the presence of a predator to the

wag-display: 1) When no predators are present, the wag-display is rarely performed; 2) When a predator is experimentally presented, motmots immediately begin to display; 3) While a predator is present, the wag-display is repeatedly performed; 4) When a predator departs (as observed with natural predators), motmots stop performing the wag-display.

Many species perform behavioral displays when they detect predators (Cott, 1940), yet the function of predator-elicited signals at first seems paradoxical. Why would an individual risk drawing attention to itself in the presence of a predator? Broadcasting one's location is especially dangerous if the signaler does not have complete information on the location of all nearby predators, as unknown predators could take advantage of the signal information and catch the signaler unaware (Bergstrom and Lachmann, 2001). For predator-elicited communication to be maintained by selection, the benefit associated with the signal must outweigh the costs associated with drawing attention to oneself. The motmot's wag-display is likely to incur considerable costs: it is easy to detect and locate because the display involves repeated and exaggerated movements, flashing of conspicuous colors, and it is accompanied by a high amplitude clucking call, which bears the vocal signal-design of a localizable signal (Bradbury and Vehrencamp, 1998). Taken together, the visual and vocal components of the wag-display appear to be designed to draw the attention of the predator to the signaler. In fact, the ease with which one is able to detect and locate wag-displays is supported by the observation by many naturalists that the wag-display draws attention to an otherwise hidden bird (Fjeldså and Krabbe, 1990; Hilty, 2003; Jones, 2003).

When a predator is detected, the wag-display is performed by both sexes with similar probability, and with a similar number of side-to-side wags of the tail. In addition, the wag-display is performed throughout the long breeding season, performed during the non-breeding season on the wintering grounds, performed at both colonial and solitary nesting sites, and performed away from the colony on off-colony territories. In all locations, and at all times of year, the wag-display is performed in a similar manner. These results suggest that the signal value of the wag-display is similar for both sexes, and that the signal value does not change in different locations or seasons.

Evidence is most consistent with the hypothesis that the intended recipient of the wag-display is the predator, and that the display functions as a pursuit-deterrent signal. When a human approached a motmot away from the colony, the bird generally performed the wag-display regardless of the presence of potential conspecific receivers. Specifically, motmots performed the wag-display in three locations where it was unlikely that conspecifics (other than the mate) were nearby: 1) at off-colony territories where only mated pairs forage and roost, and other conspecifics rarely pass through; 2) at non-colonial nest sites where nests were separated by at least 100m, and individuals from different nests seldom interact; 3) away from the breeding colonies during the non-breeding season, when these birds no longer are gregarious. In further support of the hypothesis that the intended recipients of the display are not conspecifics, the probability and intensity of the wag-display performed by lone birds in these three locations was not different from wag-displays performed when birds were near conspecifics at the colony. In addition, Skutch's (1947)

observation that the wag-display is performed by turquoise-browed motmots in the southern subspecies, which are non-colonial, supports the hypothesis that the display is not oriented to kin or non-mate conspecifics.

The possibility that the predator-elicited wag-display functions to warn mates, also was not supported. The wag-display was performed by unpaired birds, which do not gain a selective advantage from performing the costly display. Furthermore, unpaired birds were similarly likely to perform the wag-display, and displayed at the same intensity as paired birds, and also, paired birds who were away from their mate were similarly likely to perform the wag-display, and displayed at the similar intensity, as paired birds who were near their mate.

The third hypothesis, that the predator-elicited wag-display functions as an alarm signal that directly benefits the signaler, also was not supported. When a human approached a colony of motmots, the resulting wag-display did not cause conspecifics to move closer to one another (i.e., group), or to move closer the predator (i.e., mob or flee toward predator). These results are confirmed by behavioral observations when natural predators arrived at the colony: there was no detectable mobbing, grouping, or fleeing toward the predator.

The artificial wag-display performed by the robotic mot-bot did not increase conspecific vigilance, cause departure from the colony, or elicit wag-display. Because there was no noticeable reaction by conspecifics to the wag-display, these results suggest that conspecifics are not the intended recipients of the signal; however, I am hesitant to place too much weight on this line of evidence, as these negative results may have arisen because the mot-bot was not perceived as a living conspecific. Although,

it is worth noting that the mot-bot was once attacked by a nearby motmot (before it performed the wag-display), which suggests that the mot-bot was indeed perceived as a live conspecific.

The wag-display fulfils the signal design criteria of a pursuit-deterrent signal because the wag-display is easy to locate, which is in sharp contrast to the design features of some warning alarm signals, which reduce localizability (Marler, 1955). It is also worth noting that visual signals are not likely to function as conspecific alarm signals since they require conspecific receivers to be looking at the signaler, and are thus less effective than vocal signals at communicating alarm (Woodland et al., 1980).

Many species perform pursuit-deterrent signals in order to deter predators from ambush (Artiodactyls, Caro et al., 2004; Great Gerbil (*Rhombomys opimus*): Randal et al., 2000; Kangaroo Rats (*Dipodomys*): Randall and Boltas King, 2001), and in some cases pursuit-deterrent signals are selectively given only in the presence of predators who hunt by ambush (i.e. cats and birds-of-prey) and are not performed in the presence of predators which do not rely on stealth and ambush (Diana Monkeys (*Cercopithecus diana*): (Zuberbühler et al., 1997). Ambush predators have been shown to abandon hunting when prey are aware of their presence. Such abandonment has been demonstrated by Elliot et al. (1977), who showed that African Lions (*Panthera leo*) do not stalk animals which were aware of their presence, and by Schaller (1967), who showed that barking in deer causes tigers (*Panthera tigris*) to rise from concealment and walk away.

Although pursuit-deterrent signals have only been reported for a few avian species (Alvarez, 1993; Cresswell, 1994b; Laiolo et al., 2004, Spitznagel, 1996; Woodland et al., 1980), they may be especially relevant in avian species like motmots, which are frequently preyed upon by ambush predators such as bird-hawks, foxes, and small cats. Because the turquoise-browed motmot is rather large and a slow flyer, two life-history characters make the species especially susceptible to ambush predators: 1) they place their tunnel-nest near or on the ground, and 2) motmots commonly forage on the ground and restrict their foraging attempts to small areas, frequently using the same perch between repeated sallies. As a result, motmots make many repeated movements in small areas, which may make them especially susceptible to predators that lie in wait where they anticipate their prey to occur. Because ambush predators rely on being hidden or undetected while hunting, a pursuit-deterrent signal could effectively dissuade such predators from attempting ambush. It is likely that the motmot's wag-display functions as a perception advertisement that communicates the bird's awareness of the predator, and also the bird's preparedness to escape.

If the motmot's wag-display does inform ambush predators that they have been detected, it might be more appropriate to think of the wag-display as an ambush-deterrent, rather than a pursuit-deterrent signal. Although the data presented in this paper are consistent with the pursuit/ambush-deterrent hypothesis, to fully test this hypothesis it will be necessary to experimentally present natural predators with motmots who wag-display and who do not wag-display. I predict that mammalian and

avian predators who rely on ambush will be less likely to attempt an ambush on a motmot that has been observed performing the wag-display.

Pre-feeding Wag-display

In its second context, the wag display is occasionally performed before delivering food to nestling, yet the wag-display is not performed prior to when birds enter the nests before eggs hatch.

In 20% of cases when a male or female motmot returns to the colony from a successful foraging bout, it lands on a nearby perch often behind or above its tunnel-nest, and while perched, it performs the pre-feeding wag-display. The pre-feeding wag-display is performed by both sexes with similar probability, and with a similar number of side-to-side wags of the tail.

There is no difference in bout-length between predator-elicited, and pre-feeding wag-displays, and in both contexts, a simultaneous up-down and side-to-side motion of the tail generally precedes each bouts. The pre-feeding wag-display is, however, unique in that it is performed in the absence of predators and it is performed without vocalization.

The pre-feeding wag-display does not function to alert nestlings to the arrival of food, because the display is generally performed above and behind the nesting colony where nestlings are unable to detect the signal. There was no support for the hypothesis that the pre-feeding wag-display functions to advertise parental quality to potential mates, as neither the size of the food in the bill, nor the presence of the mate influences either the probability of performing the display, or its intensity.

Because the pre-feeding wag-display does not differ in appearance from the predator-elicited wag-display, and since there does not appear to be a separate function to the pre-feeding wag-display, I suggest that the signal may function in a similar manner when performed in both contexts. That is, the signal may function as a pursuit-deterrent signal regardless of whether it is performed when a predator is present, or when performed before a parent delivers food to nestlings.

Why do motmots perform the wag-display in the absence of predators before they feed nestlings? Perhaps the increase in the occurrence of wag-display when motmots feed nestlings arises due to an amplified risk of adult-predation when repeated and localized movements to the nest could attract the attention of ambush-predators. Such an amplified risk could lower the threshold at which a motmot responds to threatening stimuli, which would translate into an increase in the occurrence of wag-display, even in the absence of a true predation threat. Such dishonest signaling to predators could persist in this system because the dishonest form of the wag-display is performed infrequently (only when a pair has nestlings), and because predators would generally benefit by abandoning pursuit or ambush when they detected the wag-display.

If the pre-feeding wag-display is performed due to an increased risk of predation while caring for nestlings, it is curious that only 62% of individuals with nestlings were observed to perform the wag-display, and among these birds, only 38% of their feedings were preceded by the display. I suggest that the birds that performed the pre-feeding wag-display had a lower threshold to the risk of predation. Further study is required to establish what factors underlie the sensitivity to the risk of

predation, and the threshold at which the pre-feeding wag-display is performed.

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